FINAL REPORT

for

Rocky Mountain National Park, Estes Park, Colorado, USA

Population demographics, habitat utilization, critical habitats, and condition of black bears in Rocky Mountain National Park.

Roger A. Baldwin

Department of Animal and Range Sciences, Las Cruces, New Mexico, USA

and

Louis C. Bender

U.S. Geological Survey, New Mexico Cooperative Fish and Wildlife Research Unit,

and

Department of Fisheries and Wildlife Sciences and Department of Animal and Range Sciences,

Las Cruces, New Mexico, USA

December 2007

Population demographics, habitat utilization, critical habitats, and condition of black bears in Rocky Mountain National Park.

Summary

1. We evaluated home-range size, overlap, and distributional patterns of black bears in Rocky Mountain National Park (RMNP) from 2003–2006. Mean size of male home-ranges (100% MCP = 103.0 km^2) was significantly larger than female home-ranges (100% MCP = 47.3 km^2) and was larger than values reported previously for RMNP (95% MCP = 35.6 km^2), though they were within the range of expected values for the western U.S. (74.2–144.5 km^2).
2. Mean size of female home-ranges was smaller than previously reported for RMNP (95% MCP = 53.9 km^2) but still substantially larger than the western U.S. average (20.1–36.1 km^2)
3. Sizes of female home ranges were positively related to surrogates of vegetation productivity including maximum temperature (MaxTemp) and growing degree days (GDD), but negatively correlated with precipitation (Precip).
4. Seasonal home-range size did not vary within years for males or females, but was significantly different between males and females.
5. The percentage of overlap for annual female home-ranges varied across years and was strongly related to MaxTemp and loosely related to Precip and GDD.
6. Distributional patterns of female black bears varied by year; significant changes in distribution were related to MaxTemp and Precip during autumn, but not annually or for other seasons.
7. Patterns in home-range sizes of black bears in RMNP suggest lower habitat quality for black bears in RMNP when compared to other western localities. Cool, wet years increased habitat quality for black bears in RMNP, while hot, dry years reduced habitat quality for black bears.
8. Historical data (1984–1991) from RMNP included some of the lightest weights ever recorded for black bears in North America but did not include direct measures of body condition.
9. Size of black bears during the contemporary period (2003-2006) was comparable to other western U.S. populations. Also, body fat (BF) and body condition index (BCI) of black bears during the contemporary period indicated high levels of condition.
10. BCI, BF, and body weights of female black bears all increased over the last 15–20 years; similar values for males were not significant, though small sample sizes limited power.
11. Increases in black bear size and condition were most parsimoniously related to increased use of human-use areas and anthropogenic food sources.
12. We used 3 approaches to estimate population size and density of black bears in RMNP: 1) minimum number known, 2) occupancy modeling, and 3) catch per unit effort (CPUE).
13. We used information from capture and remote-sensored cameras, as well as visitor information, to derive a minimum known population estimate of 20–24 individuals. We used the median value of 22 combined with a 3,203-m area of effect around the RMNP boundary to produce a density estimate of 1.35 bears/100 km^2.

14. The best approximating occupancy model indicated that 41.2% of RMNP was occupied by black bears.
15. We combined the occupancy estimate with mean home-range size and overlap for male and female black bears to determine a density estimate of 1.29 bears/100 km^2 (90% CI = 0.16–2.41) in RMNP.
16. We also related CPUE to density estimates for 8 low-density populations using linear regression to estimate population size for black bears in RMNP. Density estimates from CPUE models (1.03 bears/100 km^2, 90% CI = 0.27–3.67) were well within the 90% CI for occupancy estimates and suggest these approaches may be useful for future population monitoring.
17. The current status of RMNP's black bear population appears to be stable to increasing (see 20 below), although distributions may be shifting toward human-use areas.
18. Black bears in RMNP exhibited earlier age of first reproduction (historical = 7.5 years, contemporary = 5.5 years) and higher cub survival (historical = 43%, contemporary = 71%) than historic values; litter size and adult and subadult survival were similar between periods.
19. Enhanced reproductive attributes resulted in higher recruitment (yearlings/female/year; historical = 0.34, contemporary = 0.56), a greater number of reproductive years (historical = 7.5, contemporary = 9.5), and higher reproductive output per female lifetime (number of cubs reaching reproductive age/female reproductive lifetime; historical = 0.73, contemporary = 1.80) for 2003–2006 data as compared to 1984–1991 data for RMNP. Current reproductive rates in RMNP are similar to other western U.S. populations.
20. Population modeling using historic and contemporary demographics predicted a much larger population size at the end of 10-year simulations for the contemporary period (90% probability of a final population size of ≤ 53 versus ≤ 19) using the same initial population size and each period's respective population age/sex structure.
21. Higher potential rate-of-population-increase in the contemporary period reflects increased productivity of the black bear population as survival rates were similar between periods.
22. This increased productivity may be related to better nutritional condition of reproductive females from the current population (weight: historical = 60 kg, contemporary = 68 kg; body fat: historical = 15%, contemporary = 23%).
23. We observed differences in the relationship between den locations and most habitat and physiographic factors (aspect, elevation, covertype, distance to roads and trails) between historic and contemporary periods in RMNP.
24. Maximum entropy modeling of den locations resulted in different habitat variables being included in the best models of suitable denning sites for the historic (slope, elevation, covertype) and contemporary periods (slope, distance to roads, aspect, canopy height) and indicate a shift in den locations over the last 15–20 years towards areas characterized by higher human presence.
25. Shifts of preferred denning locations towards areas of higher human influence supports other data (bear condition, home range locations, habitat use associations, etc.) that suggests that black bears appear to be habituating to humans.

26. Date of den entrance was most strongly influenced by age class and correlates of vegetation productivity (growing-season precipitation and temperature), with den entrance typically later for adult black bears during cooler, wetter years. Sex of black bears was loosely correlated to time of den exit; males emerged before females.
27. Most common foods of black bears as determined by adjusted volumetric values from scat analyses annually were grasses (24.2%), berries (16.8%), and ants (31.2%). Use of grasses, berries, and small mammals varied by season, with greatest use of grasses (49.1%) occurring during spring and berries (31.6%) and small mammals (14%) during autumn.
28. Focal animal observation yielded similar trends annually for time spent foraging on grasses (17.8), berries (10.2), and insects (61.3) with all 3 differing between spring and summer seasons; no analyses were conducted for autumn given small sample sizes.
29. Nutritional assessments indicated highest values for gross energy and crude fat in black bear diets during summer; no seasonal differences were noted for fecal nitrogen.
30. Gross energy was typically lowest for grasses and other herbaceous plants but highest for ants and ungulates. Fecal nitrogen was strongly related to most animal sources but was negatively correlated with vegetative matter. Crude fat showed the strongest positive relationship with berries, though this was likely influenced by the presence of seeds in the analysis.
31. Historic diets of black bears in RMNP showed greater frequency of ants but less grass, while contemporary diets included substantially greater amounts of anthropogenic foods. This increased use of human foods likely contributed to increases in observed body size (weight females: historic = 52 kg, contemporary = 58 kg), body condition (body fat females: historic = 15.0%, contemporary = 22.8%), and population growth rate (historic $\lambda = 1.01$, contemporary $\lambda = 1.11$) for the contemporary black bear population.
32. We assessed habitat selection across 3 spatial scales (landscape, home-range, and site-specific) to delineate critical habitats for black bears in RMNP for both historic (1984–1991) and contemporary populations.
33. Black bear habitat selection at both landscape and home-range scales was highly variable both historically and contemporarily, although black bears were commonly associated with aspen covertypes and human-use sites and avoided open covertypes.
34. Relationships were more consistent for landscape metrics, with black bears preferring highly diverse landscapes high in edge and comprised of small patches both in the contemporary and historic periods.
35. Nutritional condition of black bears in RMNP was most strongly positively associated with aspen, mesic shrublands, and human-use areas, while limber pine and mixed conifer had the most consistent negative influence on bear body fat and body condition indices.
36. Human-use areas were also used at a much higher rate during the contemporary period (70% of black bear locations in human-use areas) than historically (51% of black bear locations in human-use areas), suggesting increasing habituation of black bears for human influenced habitats. This trend likely was driven by high yield resource capture (i.e., anthropogenic food sources).
37. Site-specific analyses indicated that black bears preferred north and east facing aspects, greater numbers of logs and ant mounds, and less grass and woody cover at foraging sites as compared to random sites. Site-specific preferences correspond to habitat attributes that predict greater quantity and quality of plant and insect foods for black bears.

38. Few differences were found between resting and foraging locations. However, observed differences indicated a preference for steeper slopes and denser woody understory cover at resting sites. Both of these attributes relate to less disturbance and greater security.
39. Collectively, analyses suggested that small, evenly distributed patches of aspen, human-use, and mesic shrubland covertypes provided the best habitat for black bears in RMNP.
40. Covertype composition is likely less important than high habitat diversity in RMNP. Black bear distribution patterns are tied closely to actual distribution of food sources that show high annual, seasonal, and spatial variability in RMNP. By maximizing diversity within home-ranges, black bears likely assure that at least some of these components will be present in home-ranges. Black bears more frequently shift distribution during years when foods are less available due to climatic effects, further reflecting the need for high habitat diversity to ensure that at least some types of foods are available to black bears annually in RMNP.
41. Management strategies designed to provide or increase the diversity of RMNP's landscape and provide key structures associated with bear foraging (i.e., dead and down logs, etc.) may help reverse an apparent shift in black bear use to high human-use sites while maintaining increased black bear condition in RMNP.

TABLE OF CONTENTS

INTRODUCTION

Black bears (*Ursus americanus*) are a charismatic omnivore found throughout most of the western United States. Black bears occur in Rocky Mountain National Park (RMNP); however, the population is very small (< 25 individuals; see Chapter 3) and little is known of their habits or critical habitats. Because of this, RMNP staff has concerns over the viability of the bear population, preservation of which is a key management goal of the National Park Service (National Park Service 1988). Baseline data on black bear ecology collected in RMNP from 1984–1991 was summarized to provide some information about various demographic and ecological aspects of this population (Zeigenfuss 2001). However, results from this analysis were inconclusive, suggested that additional work was needed to better understand this bear population, and were limited by methods employed. Key to conserving bears in RMNP is information on what factors are critical for bear survival and reproduction. Such information is needed for management prescriptions that preserve critical areas, promote bear populations, and reduce bear/human conflicts.

RMNP's black bear population is unique; historical data suggested one of the lowest densities and reproductive rates ever recorded for black bears in North America (see Chapter 4). Additionally, sizes of bears captured from 1984–1991 was well below average (Zeigenfuss 2001). These characteristics (small individual size, low productivity) are indicators of habitats providing limited nutrition (Hanks 1981). Because RMNP is comprised almost entirely of tundra, high elevation forests, and meadows, potential food sources for bears are limited; such habitats generally lack hard mast crops and soft mast crops can be scarce and variable. Moreover, high elevations (> 2,286 m) result in short growing seasons (6–7 months/year active), limiting the time that bears have to obtain resources necessary for growth and reproduction. These characteristics suggest that habitats of RMNP may be marginal for bears.

Because of the importance of nutrition for survival and productivity of wildlife populations (Hanks 1981), potential plant composition and growth limitations in RMNP habitats makes it imperative to identify key bear use areas and critical foraging and security areas. Disturbance to or loss of these habitats could strongly affect survival and productivity of RMNP's bear population. A review of historic demographics (Zeigenfuss 2001) suggested that the bear population in RMNP was barely able to balance mortality with recruitment; thus, loss of critical areas could lower survival and productivity resulting in the loss of bears from RMNP. However, this assumes that historic demographics still apply to black bears in RMNP in the contemporary period. No data exists since the 1984–1991 period to indicate whether attributes such as individual or population size, survival, or productivity of the bear population has changed in RMNP over the last approximately 20 years.

Little empirical data exists on how habitat influences body condition of black bears. Knowledge of how organisms utilize, and what they derive from, habitat is essential in understanding productivity and survival of wildlife (Hanks 1981, Morrison et al. 1992). Many studies (i.e., Hugie 1982, Reynolds and Beecham 1980, Rogers 1987, Elowe and Dodge 1989, Samson and Huot 1995) have noted a strong relationship between habitat quality and bear productivity. However, others contend that this relationship is based on either inappropriate or inaccurate data (Kolenosky 1990, Beck 1991). More importantly, none have quantified the basic habitat-condition linkage. Quantifying this relationship is important because survival and productivity can be affected by a variety of non-habitat factors including human intolerance. However, a population must achieve a high level of condition to maximize productivity (Gaillard et al. 2000). If bears in RMNP still show smaller body size and low productivity, it is almost certainly a nutritional effect, and consequently habitats that provide better nutrition for bears need to be identified and actively promoted.

Because of the above, use of direct measures of body condition to assess the inherent value of habitats (i.e., ability of bears to accrue fat or other endogenous energy reserves based on availability of certain habitat attributes) is critical to identifying important habitats and habitat components for bears in RMNP. Several studies (i.e., Davis 2005, Bender et al. 2007) have found that body condition of ungulates was predictable from habitat attributes such as vegetation cover types or understory productivity. This approach has not been used on bears, but has the potential to yield similar results. Because animal condition is a powerful indicator of habitat quality (Hanks 1981, Franzmann 1985, Bender and Cook 2005, Bender et al. 2007), knowing what habitats and critical areas contributed to varying condition of individuals allows direct identification of critical habitats.

Given the potentially tenuous status of black bears in RMNP as projected by historic data on size and productivity, identifying what is affecting bear condition and population performance is important in developing management strategies for black bears in RMNP. Therefore, our purpose was to quantify current population status and demographics of black bears in RMNP, and to identify important habitat-condition relationships and consequently critical habitats of black bears in RMNP. Our goal was to use this information to develop methods to monitor black bear trends and habitat associations in RMNP, and to identify management strategies to provide or enhance critical habitats of bears in RMNP. Our specific research questions included:

1. *What is the nutritional condition of black bears in RMNP?*
2. *What are the diets and diet quality of black bears in RMNP?*

3. *What is the survival and productivity of black bears in RMNP?*
4. *What is the population size and trend of black bears in RMNP?*
5. *What is the relative production and distribution of bear foods in RMNP?*
6. *What are the activity patterns of black bears in RMNP?*
7. *What are the site, home range, and landscape level habitat attributes associated with habitat use patterns of black bears in RMNP?*
8. *What are critical habitats for black bear survival, productivity, and condition in RMNP?*

STUDY AREA

Rocky Mountain National Park is a 1,080 km^2 biosphere reserve located in the Rocky Mountain Front Range of northcentral Colorado. Topography in RMNP was shaped by glaciation, and consists of high mountainous peaks interspersed with small subalpine meadows, lakes, streams, glaciers, and tundra at higher elevations. Elevations range from 2,400–4,345 m. The continental divide bisects RMNP, creating different climatic patterns to the east and west. The eastern Park is drier, with precipitation averaging 35.1 cm in Estes Park. Western RMNP is more mesic, with precipitation averaging 50.8 cm in Grand Lake. Seventy-five percent of precipitation falls from April to September. In Estes Park, mean daily high temperatures range from 3.6º C in January to 25.7º C in July.

Vegetation in RMNP consists of > 700 plant species. Lower slopes and valleys are comprised of forests of lodgepole (*Pinus contorta*) and ponderosa pine (*P. ponderosa*), blue spruce (*Picea pungens*), Douglas-fir (*Psuedotsuga menziesii*), juniper (*Juniperus* spp.), and aspen (*Populus tremuloides*) interspersed with bunchgrass and sedge-dominated herbaceous meadows. At higher elevations, subalpine forests of Engelmann spruce (*P. englemannii*) and subalpine fir (*Abies bifolia*) predominate. Elevations above timberline are dominated by tundra and bare rock. Wildlife in RMNP includes a diverse fauna dominated by large mammals including black bear, elk, mule deer (*Odocoileus hemionus*), moose (*Alces alces*), Rocky Mountain bighorn sheep (*Ovis canadensis*), mountain lion (*Puma concolor*), bobcat (*Lynx rufus*), and coyote (*Canis latrans*).

LITERATURE CITED

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

Bender, L. C., and J. G. Cook. 2005. Nutritional condition of elk in Rocky Mountain National Park. Western North American Naturalist 65:329–334.

Bender, L. C., L. A. Lomas, and T. Kamienski. 2007. Habitat effects on condition of mule deer in arid mixed woodland-grassland. Rangeland Ecology and Management 60:277–284.

Davis, R. W. 2005. A GIS-based habitat model for predicting elk nutritional condition in the Pacific Northwest. Dissertation, University of Illinois, Urbana, Illinois, USA.

Elowe, K. D., and W. E. Dodge. 1989. Factors affecting black bear reproductive success and cub survival. Journal of Wildlife Management 53:962–968.

Franzmann, A. W. 1985. Assessment of nutritional status. Pages 239–260 *in* R. J. Hudson and R. G. White, editors. Bioenergetics of wild herbivores. CRC Press, Boca Raton, Florida, USA.

Gaillard, J.-M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toïgo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31:367–393.

Hanks, J. 1981. Characterization of population condition. Pages 47–73 *in* C. W. Fowler and T. D. Smith, editors. Dynamics of large mammal populations. The Blackburn Press, Caldwell, New Jersey, USA.

Hugie, R. D. 1982. Black bear ecology and management in the northern conifer-deciduous forest of Maine. Dissertation, University of Montana, Missoula, Montana, USA.

Kolenosky, G. B. 1990. Reproductive biology of black bears in east-central Ontario. International Conference on Bear Research and Management 8:385–392.

Morrison, M. L., B. G. Marcot, and R. W. Mannan. 1992. Wildlife-habitat relationships: concepts and applications. First edition. The University of Wisconsin Press, Madison, Wisconsin, USA.

National Park Service. 1988. Management policies. U. S. Department of the Interior, Washington D. C., USA.

Reynolds, D. G., and J. J. Beecham. 1980. Home range activities and reproduction of black bears in west-central Idaho. International Conference of Bear Research and Management 4:181–190.

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.

Zeigenfuss, L. C. 2001. Ecology of black bears in Rocky Mountain National Park: an analysis of population dynamics, diet, and habitat selection (1985–1991). Unpublished report, U.S. National Park Service, Rocky Mountain National Park, Colorado, USA.

Chapter 1:

Home-range size, overlap, and distributional patterns of black bears in Rocky Mountain National Park, Colorado

Roger A. Baldwin, Department of Animal and Range Sciences, New Mexico State University, P.O. Box 30003 MSC 4901, Las Cruces, New Mexico 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, New Mexico 88003, USA

Chapter summary: Knowledge of spacing and distribution of black bears (*Ursus americanus*) can lead to a greater understanding of their use of available resources. We evaluated home-range size, overlap, and distributional patterns of black bears in Rocky Mountain National Park (RMNP) from 2003–2006. Size of male home-ranges (100% MCP = 103.0 km^2; 95% MCP = 77.9 km^2) was significantly larger than female home ranges (100% MCP = 47.3 km^2; 95% MCP = 32.3 km^2) and was larger than values reported previously for RMNP (95% MCP = 35.6 km^2), though within the range of expected values for the western U.S. (74.2–144.5 km^2). Although contemporary female home-ranges in RMNP were smaller than recorded historically (95% MCP = 53.9 km^2), they were still substantially larger than the western U.S. average (20.1–36.1 km^2). Size of female home-ranges was positively related to maximum temperature (MaxTemp) and growing degree days (GDD), but negatively correlated with precipitation (Precip). Seasonal home-range size did not vary within years for males or females, but was significantly different between males and females. Spring, summer, and autumn female home-range sizes were not related to climatic factors; collectively, average seasonal home-range size was positively related to MaxTemp. The percentage of overlap for annual female home-ranges varied across years and was strongly positively related to MaxTemp and loosely negatively related to Precip and positively to GDD. Seasonal overlap was substantially different between spring-summer and spring-autumn seasons, but not summer-autumn. As with seasonal home-range size, separate seasons were not correlated to climatic factors, though collectively, MaxTemp was positively related to overlap seasonally. Distributional patterns of female black bears varied by year with differences primarily driven by a shift in home-ranges during autumn; significant changes in distribution were positively related to MaxTemp and Precip during autumn, but not annually or for other seasons. Collectively, data suggest lower habitat quality for black bears in RMNP when compared to other western localities. Although cool, wet years increased habitat quality, black bear populations in RMNP will likely be limited to levels reflective of hot, dry years unless black bear distributions shift to areas less affected by natural climatic variations in food resource availability.

Knowledge of spacing and distribution of black bears (*Ursus americanus*) can lead to a greater understanding of their use of available resources. Determining home-range size, degree of home-range overlap, and temporal and spatial distributional patterns provides a first step in understanding this relationship. Home-range shape and size is influenced by many factors including abundance and distribution of foods (Lindzey and Meslow 1977, Garshelis and Pelton 1981, Rogers 1987, Schwartz and Franzmann 1991, Powell et al. 1997, Samson and Huot 1998, Koehler and Pierce 2003), population densities (Alt et al. 1980, McLoughlin et al. 2000, Oli et al. 2002, Pelton 2003), sex and age class of individuals (Jonkel and Cowan 1971, Lindzey and Meslow 1977, Alt et al. 1980, Rogers 1987, Powell et al. 1997, Hirsch et al. 1999, Koehler and Pierce 2003), social status (Alt et al. 1980, Bunnell and Tait 1981, Powell et al. 1997, Koehler and Pierce 2003), and procedures used to determine the bear's home-range (White and Garrott 1990, Powell 2000, Pelton 2003). Because of the dynamic interaction of these factors, there can be large variation in the size of black bear home-ranges. Home-range sizes are almost always larger for males than females (typical range = 22–1,721 km^2 for males, 5–49 km^2 for females; Pelton 2000), although this difference is not always pronounced (e.g., Lindzey and Meslow 1977, Garshelis and Pelton 1981). Subadult home-ranges are generally smaller (Alt et al. 1980).

Historic data in Rocky Mountain National Park (RMNP) indicated an average home-range size of 53.9 km^2 for female black bears and 35.6 km^2 for males (Zeigenfuss 2001). Home-ranges reported for females in RMNP were larger than those reported for most other black bear populations. More than any other factor, habitat quality, specifically abundance and distribution of food, has been linked to home-range size (Lindzey and Meslow 1977, Reynolds and Beecham 1980); the lower the quality of habitat, the greater the home-range size. Therefore, these large historic home-ranges suggest that food availability was limited in RMNP.

The amount of overlap in female black bear home-ranges is also indicative of habitat quality. Typically, territoriality in females is minimal in locations with abundant or sparse food production, but is present to varying degrees when food abundance is intermediate (McLoughlin et al. 2000). Additionally, distributional patterns of black bears are likely to vary by year and season (Garshelis and Pelton 1981, Rogers 1987, Samson and Huot 2001). Relating food production to female home-range size, overlap, and distributions should provide valuable insight into the potential of available habitats to support the contemporary black bear population in RMNP. However, determining food abundance across years is expensive and time consuming. Alternatively, climatic factors such as temperature and precipitation have been correlated to vegetative production (e.g., Polis et al. 1997, DeYoung et al. 2000, Koehler and Pierce 2003) and may provide a viable means for assessing this relationship.

My goal was to determine temporal patterns in home-range size, overlap, and distribution to provide insight into how black bears utilize the landscape of RMNP. My specific objectives included: 1) determine size of male and female home-ranges annually and by season; 2) assess amount of overlap between female home-ranges annually and by season; 3) determine distributional patterns of female black bears annually and by season; and 4) relate home-range size, overlap, and distribution to climatic factors.

METHODS

I used modified Aldrich foot snares and culvert traps to capture black bears from 2003–2006. I immobilized bears with a 5:1 mixture of ketamine hydrochloride and xylazine hydrochloride (200 mg ketamine and 40 mg xylazine per ml) and fit bears with radiocollars. I radiotracked all collared individuals approximately 1 week after capture until den entrance. In years after capture, I radiotracked individuals from late May through the time of den entrance. I obtained locations of radiocollared bears as often as possible, with locations typically recorded a minimum of once per week. However, due to logistical constraints and movements off RMNP property, this time interval was occasionally longer. Due to this occasional lag in location frequency and frequent forays of black bears off RMNP, I considered estimated home-range sizes to be the minimum area used by black bears.

I determined fixes of black bears through direct observation. When direct observation was not possible, I circled the bear to determine its location, and estimated the distance to the bear based on the radius of the circle. Most locations were within 200 m of the bear, though occasionally insufficient time or inaccessible bear locations resulted in greater distances.

I used 100% and 95% minimum convex polygon (MCP) and 95% adaptive kernel (ADK) approaches for estimating annual home-range size. All home-ranges were constructed in ArcView 3.3 (Environmental Systems Research Institute, Redlands, California, USA). The 100% MCP approach utilized all locations and constructed a convex polygon around the outer locations (Mohr 1947). For 95% MCP home-ranges, I used the area added approach to exclude outlier locations (White and Garrott 1990). I derived 95% ADK home-ranges using the least-squares cross-validation method for selecting the appropriate smoothing factor (Worton 1995, Seaman et al. 1999). I tested for differences in male and female seasonal home-range sizes using Mann–Whitney *U*-tests (Zar 1999). I assessed annual overlap of female black bear home-ranges using 95% MCP home-ranges to remove the influence of outliers. I weighted the amount of overlap for each female by the size of its home-range to reduce the impact of varying home-range sizes and to yield a mean percentage of the entire area of overlapping female home-ranges.

For seasonal home-ranges, I used the 100% MCP estimator, as sufficient numbers of locations were not available for other estimators. I tested for differences in male and female seasonal home-range sizes using Mann–Whitney *U*-tests (Zar 1999). I also used the Kruskal–Wallis test (Zar 1999) to assess differences in home-range size for both males and females across seasons. I assessed the amount of seasonal overlap of female home-ranges in the same manner as that described for annual overlap. I used the Kruskal–Wallis test (Zar 1999) to assess differences in home-range overlap across seasons.

Maximum daily temperature (MaxTemp), precipitation (Precip), and growing degree days (GDD; a heat index that relates plant growth to air temperature) were compared to annual and seasonal home-range size and overlap using linear regression (Zar 1999) to assess their influence on these parameters. Climatic factors were recorded daily in Estes Park, Colorado, from 1 April–31 October, 2003–2006; mean values were used for MaxTemp and GDD, while total values were used for Precip. All weather variables were obtained from the National Climatic Data Center as compiled by Weather Source (http://weather-source.com).

I also compared distribution of annual home-ranges across years and seasonal home-ranges of female black bears within and across years using multi-response permutation procedures (MRPP) in program BLOSSOM (Slauson et al. 1991). This approach measures Euclidean distances within a specified group and compares these values to randomly generated distances to test for differences between ≥ 2 years or seasons (Berry and Mielke 1983). I used a preset $\alpha = 0.10$ with a Bonferroni correction for multiple comparisons for each bear to assess significance. Additionally, I related the change in mean MaxTemp, total Precip, and mean GDD to MRPP results across years using logistic regression (1 = altered distribution, 0 = similar distribution) (Hosmer and Lemeshow 2000) to assess correlates between these factors and home-range distribution. Climatic factors included data from 1 April–31 May for the spring season, 1 April–31 July for summer, and 1 April–31 October for the autumn season to relate cumulative precipitation and temperature effects during the vegetative growing season on home-range size, overlap, and distribution. Because of substantial differences in 1 April–31 October MaxTemp

(2004 = 17.7º C; others = 19.8º C [SE = 0.2]) and Precip (2004 = 53.1 cm; others = 29.5 cm [SE = 2.9]) between 2004 and all other years, I also compared the number of significant distributional shifts of female black bear home-ranges between 2004 and other surveyed years (Fisher's exact test; Zar 1999) to assess the influence of these climatic factors on home-range shifts both annually and seasonally.

RESULTS

I collected 643 total locations of 11 (6 females, 5 males) black bears from 2003–2006, with the majority 84% of fixes within 200 m of the bear's location (84%). An additional 3 black bears were captured but either lost their collar or left the study area within 2 weeks of capture. The number of annual locations ranged from 10–28 ($\bar{x}$ = 18.0, SE = 2.4) for adult males and 12–53 ($\bar{x}$ = 27.3, SE = 2.9) for females and allowed determination of 6 male and 14 female annual home-ranges from 2004–2006. Additionally, I constructed annual home-ranges for 2003 for comparative purposes but excluded them from analyses unless otherwise noted due to late capture dates resulting in a lack of year-long locations. I found no difference between home-range size for adult and subadult females (100% MCP: U = 31.0, P = 0.298; 95% MCP: U = 27.0, P = 0.606; 95% ADK: U = 26.0, P = 0.699) and thus combined them for further analyses. Pooled home-ranges among years were larger for adult males than for females (100% MCP: U = 74.0, P = 0.006; 95% MCP: U = 74.0, P = 0.006; 95% ADK: U = 75.0, P = 0.005) and subadult males (Table 1). Given the high number of locations recommended for 95% kernel estimators (30–50 locations; Seaman et al. 1999), I felt the 95% MCP more accurately reflected home-range size in RMNP and used these estimates in subsequent analyses. Given this, I may have underrepresented the size of home-ranges, though a comparison of plots suggested 95% MCP

Table 1.1. Mean home-range size (km^2) and associated standard errors (SE) for black bears in Rocky Mountain National Park, Colorado, 2004–2006. Home-range estimators included 100% (100MCP) and 95% (95MCP) minimum convex polygon and 95% adaptive kernel (95ADK). Adult (Ad) and subadult (Sub) females also were combined (Female) as no difference was detected ($P >$ 0.25).

Year	Method	Ad male	SE	Sub male	SE	Ad female	SE	Sub female	SE	Female	SE
2004	100MCP	71.5	1.6	15.5	N/A[a]	23.3	12.1	30.8	16.5	26.7	8.6
	95MCP	52.5	0.8	8.7	N/A	12.0	4.2	26.1	16.0	17.6	6.5
	95ADK	213.0	124.2	72.1	N/A	24.7	8.0	72.0	14.6	43.6	13.2
2005	100MCP	112.4	55.0	—	—	58.8	10.9	61.0	30.7	59.7	11.4
	95MCP	84.2	43.0	—	—	41.7	1.7	44.5	21.6	42.8	6.9
	95ADK	174.8	97.3	—	—	84.1	7.0	116.4	48.9	97.0	17.8
2006	100MCP	147.5	—	—	—	70.4	15.3	21.2	N/A	58.1	16.4
	95MCP	124.3	—	—	—	43.2	10.1	19.7	N/A	37.3	9.2
	95ADK	147.7	—	—	—	69.6	11.4	59.8	N/A	67.1	8.4
$\bar{x}$	100MCP	103.0[b]	18.4	15.5	N/A	50.8	9.6	41.0	13.8	47.3	7.7
	95MCP	77.9[b]	15.6	8.7	N/A	32.3	6.0	32.2	9.9	32.2	5.0
	95ADK	174.1[b]	43.3	72.1	N/A	59.5	10.0	87.3	20.2	69.4	9.9

[a] N/A = mean based on 1 individual.

[b] Includes 1 individual with locations collected from July 2005–June 2006 as MRPP results ($\delta = -0.732$, $P = 0.221$) showed no difference between partial years.

home-range curves began to plateau around 15–20 annual locations. MaxTemp ($F_{1,1}$ = 78.3, P = 0.072) and GDD ($F_{1,1}$ = 4869.3, P = 0.009) were positively correlated to 95% MCP annual female home-range size, whereas Precip ($F_{1,1}$ = 90.1, P = 0.067) was negatively correlated to annual female home-range size (Table 2).

Female black bears exhibited varying levels of home-range overlap depending on estimator and year (Table 3). As with home-range size, MaxTemp ($F_{1,1}$ = 203.2, P = 0.045) was positively correlated with female home-range overlap, but home-range overlap was less related to Precip ($F_{1,1}$ = 11.4, P = 0.183) and GDD ($F_{1,1}$ = 34.7, P = 0.107) (Table 2). Although I was not able to calculate annual home-range sizes for 2003, the percentage of overlap between female home-ranges may have been representative of the entire year. Including these values strengthened relationships between overlap and all climatic factors (MaxTemp: $F_{1,2}$ = 24.5, P = 0.038, R^2 = 0.925, β = 13.0, SE = 2.6; Precip: $F_{1,2}$ = 5.8, P = 0.137, R^2 = 0.744, β = –1.0, SE = 0.4; GDD: $F_{1,2}$ = 66.4, P = 0.015, R^2 = 0.971, β = 12.8, SE = 1.6).

For seasonal home-range size, the number of locations ranged from 4–14 (spring: $\bar{x}$ = 6.0, SE = 0.5; summer: $\bar{x}$ = 6.9, SE = 1.2; autumn: $\bar{x}$ = 7.2, SE = 0.4) for adult males and 4–27 (spring: $\bar{x}$ = 8.5, SE = 1.0; summer: $\bar{x}$ = 11.9, SE = 1.7; autumn: $\bar{x}$ = 11.4, SE = 1.3) for females. I only used bears in which I collected a minimum of 4 locations per season as plots suggested home-range size began to plateau at 4–6 locations. This resulted in 46 (spring = 12, summer = 17, autumn = 17) seasonal home-ranges for females and 21 (spring = 6, summer = 8, autumn = 7) seasonal home-ranges for males for analyses. Neither male (H_2 = 1.2, P = 0.551) nor female (H_2 = 1.0, P = 0.615) home-range size differed across seasons. As with annual home-ranges, seasonal home-range sizes were larger for adult males than females (U = 473.0, P = 0.032) (Table 4). No significant relationships were found between spring ($F_{1,1}$ < 1.5, P > 0.40), summer

Table 1.2. Results of regression modeling comparing annual and seasonal home-range size (km^2) and overlap for female black bears in Rocky Mountain National Park, Colorado during 2004–2006 to mean maximum temperature (° C), total precipitation (cm), and growing degree days (a heat index that relates plant growth to air temperature) collected from 1 April–31 October for each respective year. Annual and seasonal home-ranges represent 95% and 100% minimum convex polygons, respectively. Significant models are in bold.

Model	Variable	*F*	*P*	R^2	β	SE
Annual HR size	**Maximum temperature**	**78.3**	**0.072**	**0.987**	**10.981**	**1.241**
	Precipitation	**90.1**	**0.067**	**0.989**	**–1.095**	**0.115**
	Growing degree days	**4869.3**	**0.009**	**1.000**	**9.782**	**0.140**
Annual HR overlap	**Maximum temperature**	**203.2**	**0.045**	**0.995**	**14.795**	**1.038**
	Precipitation	11.4	0.183	0.920	–1.417	0.419
	Growing degree days	34.7	0.107	0.972	12.944	2.199
Seasonal HR size	**Maximum temperature**	**20843.6**	**0.005**	**1.000**	**8.360**	**0.058**
	Precipitation	21.9	0.134	0.956	–0.815	0.174
	Growing degree days	**119.4**	**0.058**	**0.992**	**7.370**	**0.675**
Seasonal HR overlap	**Maximum temperature**	**237.4**	**0.041**	**0.996**	**5.557**	**0.361**
	Precipitation	11.9	0.180	0.922	–0.533	0.155
	Growing degree days	37.0	0.104	0.974	4.864	0.800

Table 1.3. Mean percentage overlap of female black bear home-ranges in Rocky Mountain National Park, Colorado, 2003–2006 using 100% (100MCP) and 95% (95MCP) minimum convex polygon and 95% adaptive kernel (95ADK) estimators.

Year	*n*	100MCP	95MCP	95ADK
2003	5	19.9	25.7	37.7
2004	5	13.6	0.9	28.9
2005	5	49.5	36.2	66.5
2006	4	33.2	22.6	12.8
$\bar{x}$ (SE)		39.8 (8.0)	32.5 (7.4)	35.6 (11.3)

Table 1.4. Seasonal 100% minimum convex polygon home-range size (km^2) and associated standard errors (SE) for black bears in Rocky Mountain National Park, Colorado, 2003–2006.

Sex	Year	Spring	SE	Summer	SE	Autumn	SE	$\bar{x}$	SE
Female	2003	—	—	6.6	5.6	12.1	4.0	10.1	3.2
	2004	8.7	4.1	6.9	2.0	6.1	3.2	7.1	1.6
	2005	18.4	1.9	36.7	13.3	24.7	6.7	26.7	5.3
	2006	19.3	3.4	16.8	4.3	25.3	12.7	20.5	4.3
	$\bar{x}$	16.2	2.0	17.9	5.0	16.8	3.9	17.1	2.3
Adult male	2003	—	—	—	—	18.4	N/A	18.4	N/A
	2004	25.6	N/A[a]	22.5	19.7	23.9	N/A	23.6	8.1
	2005	26.8	6.6	49.9	37.6	53.0	40.6	44.2	17.4
	2006	67.8	20.3	32.3	20.4	42.8	18.3	47.6	11.0
	$\bar{x}$	43.0	12.2	37.1	16.2	38.9	13.0	40.6	8.3
Subadult male	2003	—	—	—	—	7.3	N/A	7.3	N/A
	2004	9.6	N/A	0.8	—	—	N/A	5.2	4.4
	2005	—	—	—	—	—	—	—	—
	2006	—	—	—	—	—	—	—	—
	$\bar{x}$	9.6	N/A	0.8	N/A	7.3	N/A	5.9	2.6

[a] N/A = mean based on 1 individual.

($F_{1,1} < 1.0$, $P > 0.50$), and autumn ($F_{1,2} < 3.5$, $P > 0.20$) home-range sizes and climatic factors, though averages across seasons (MaxTemp: $F_{1,1} = 20843.6$, $P = 0.005$; Precip: $F_{1,1} = 21.9$, $P = 0.134$; GDD: $F_{1,1} = 119.4$, $P = 0.058$) indicated trends similar to those reported for annual home-ranges (Table 2).

I was able to assess minimum home-range overlap for 6 individual females yielding overlap data for 45 (spring = 12, summer = 16, autumn = 17) seasonal home-ranges (Table 5). I detected a seasonal difference in overlap of female home-ranges ($H_2 = 6.1$, $P = 0.048$); these differences were observed for spring-autumn ($P = 0.035$), but not between spring-summer ($P = 0.163$) or summer-autumn ($P = 0.428$). Once again, I did not observe a significant relationship between home-range overlap for individual seasons and climatic factors ($F_{1,1} \leq 1.1$, $P \geq 0.45$), but observed similar patterns (MaxTemp: $F_{1,1} = 237.4$, $P = 0.041$; Precip: $F_{1,1} = 11.9$, $P = 0.180$; GDD: $F_{1,1} = 37.0$, $P = 0.104$) as annual home-range overlap for average seasonal overlap (Table 2).

Female black bears utilized different areas across years (Table 6), with distributions substantially different (Fisher's exact $P = 0.011$) in 2004 when compared to 2005 and 2006 (62.9% [$n = 35$] and 40.0% [$n = 30$] of home-range distributions significantly different, respectively). These differences were primarily influenced by distributional shifts during autumn (2004 = 75.0% of ranges showed a significant shift [$n = 12$], other years = 33.3% [$n = 12$]; Fisher's exact $P = 0.044$); there was little difference in significant changes in distributions during spring (2004 = 54.5% [$n = 11$], other years = 50.0% [$n = 10$]; Fisher's exact $P = 0.330$) and summer (2004 = 0.0% [$n = 4$], other years = 25.0% [$n = 4$]; Fisher's exact $P = 0.500$) between 2004 and other years (Table 6). Additionally, I found no relationship between climatic factors and spring, summer, and annual distributions ($P \geq 0.20$). However, differences in MaxTemp

Table 1.5. Mean percentage overlap of female black bear seasonal home-ranges in Rocky Mountain National Park, Colorado from 2003–2006 using a 100% minimum convex polygon estimator.

Year	Spring	Summer	Autumn	$\bar{x}$ (SE)
2003	—	0.0	5.9	3.0 (3.0)
2004	4.7	2.6	0.7	2.7 (1.1)
2005	0.0	33.2	14.6	15.9 (9.6)
2006	0.03	0.0	32.7	10.9 (10.9)
$\bar{x}$ (SE)	1.6 (1.6)	8.9 (8.1)	13.5 (7.0)	8.6 (3.9)

Table 1.6. Multi-response permutation procedure results (δ) for shifts in spring (Sp), summer (Sm), autumn (Au), and annual (An) home-range distributions among years for female black bears in Rocky Mountain National Park, Colorado, 2003–2006.

	Bear	Total	2003–04	2003–05	2003–06	2004–05	2004–06	2005–06
Sp	2	–3.2	—	—	—	0.1	–2.1	–4.5
		(0.009)*	—	—	—	(0.437)	(0.043)	(0.003)*
	3	—	—	—	—	—	—	–0.3
		—	—	—	—	—	—	(0.282)
	4	—	—	—	—	—	—	–2.6
		—	—	—	—	—	—	(0.023)
	6	–0.1	—	—	—	0.1	–0.9	0.1
		(0.388)	—	—	—	(0.469)	(0.182)	(0.469)
Sm	2	–15.8	–10.2	–8.5	–18.8	–4.1	–1.6	–9.9
		(<0.001)*	(<0.001)*	(<0.001)*	(<0.001)*	(0.004)*	(0.071)	(<0.001)*
	3	–3.8	0.5	–2.3	–4.4	–0.8	–3.8	–1.6
		(0.003)*	(0.600)	(0.035)	(0.003)*	(0.173)	(0.005)*	(0.075)
	4	–6.8	–4.0	–2.6	–1.9	–3.9	–4.9	–3.9
		(<0.001)*	(0.004)*	(0.027)	(0.054)	(0.005)*	(0.001)*	(0.007)*
	6	0.9	—	—	—	0.5	0.5	0.7
		(0.814)	—	—	—	(0.616)	(0.639)	(0.756)
Au	2	–10.2	–5.3	–2.5	–12.9	–4.2	–1.3	–7.6
		(<0.001)*	(0.001)*	(0.029)	(<0.001)*	(0.003)*	(0.108)	(<0.001)*
	3	–5.1	–5.3	–1.3	–1.8	–3.8	–1.5	–1.1
		(<0.001)*	(0.002)*	(0.100)	(0.052)	(0.004)*	(0.084)	(0.125)
	4	–9.7	–3.8	–2.8	–10.7	–1.8	–7.1	–5.4
		(<0.001)*	(0.009)*	(0.017)	(<0.001)*	(0.056)	(<0.001)*	(0.001)*
	6	–5.2	–6.6	0.4	–2.3	–3.8	–3.3	–1.8
		(<0.001)*	(0.001)*	(0.618)	(0.031)	(0.006)*	(0.011)*	(0.050)
An	2	–14.6	—	—	—	–6.6	–5.4	–16.3
		(<0.001)*	—	—	—	(<0.001)*	(0.001)*	(<0.001)*
	3	–3.7	—	—	—	–2.0	–3.9	–1.4
		(0.004)*	—	—	—	(0.049)	(0.006)*	(0.090)
	4	–9.1	—	—	—	–3.9	–11.0	–4.6
		(<0.001)*	—	—	—	(0.006*	(<0.001)*	(0.004)*
	6	–3.3	—	—	—	–4.0	–3.2	0.8
		(0.008)*	—	—	—	(0.005)*	(0.012)*	(0.814)

* Indicates a significant relationship at $\alpha = 0.017$ (0.10/6); *P*-values are listed in parentheses.

($\chi^2 = 5.8$, $P = 0.016$, $R^2 = 0.368$; $\beta = 1.534$ [SE = 0.638]; odds ratio = 4.6 [95% CI = 1.3–16.2]) and Precip ($\chi^2 = 4.4$, $P = 0.035$, $R^2 = 0.271$; $\beta = 0.114$ [SE = 0.054]; odds ratio = 1.12 [95% CI = 1.01–1.25]) were related to changes in distribution during the autumn season across years; black bears were more likely to shift distributions during warmer and wetter autumns. Individual female distributions tended to shift less within a given year, though seasonal shifts were more apparent between summer and autumn (Table 7); no shifts were observed between spring and summer.

DISCUSSION

Historic data (1984–1991) in RMNP indicated that home-range size of female black bears was among the largest reported for black bears in the western U.S. (95% MCP = 53.9 km^2; Zeigenfuss 2001). Contemporary results indicated that home-range size of females decreased in the last 10–15 years, although average size of female home-ranges was still well above the western U.S. average (Table 8), as the average 100% MCP home-range of females in RMNP was well outside the 95% CI of average home range size of females from all other western U.S. studies. In fact, 100% MCP home-ranges of female black bears in RMNP were larger than all but 2 studies listed in Table 8, and those studies each had only 2 females monitored, limiting inferences from their results (Nevada, Goodrich 1990; Montana, Aune 1994). Numerous investigators have noted that home-range size is typically larger in areas where food abundance is limited (e.g., Lindzey and Meslow 1977, Reynolds and Beecham 1980). Because direct estimates of forage productivity were not available for all years in RMNP (see Chapter 7), I used climatic factors as surrogates (Polis et al. 1997, DeYoung et al. 2000, Koehler and Pierce 2003). Relationships between MaxTemp, Precip, and GDD indicated that cooler, wetter years resulted

Table 1.7. Multi-response permutation procedure (δ) results with corresponding P-values (P) for seasonal distributions of female black bears within years in Rocky Mountain National Park, Colorado, 2003–2006.

		Annual		Spring–Summer		Spring–Autumn		Summer–Autumn	
Bear	Year	δ	P	δ	P	δ	P	δ	P
2	2003	—	—	—	—	—	—	–9.4	<0.001*
	2004	–1.8	0.052	–1.5	0.085	–1.4	0.098	–0.8	0.184
	2005	1.4	0.975	0.7	0.727	0.7	0.737	1.4	1.000
	2006	–0.6	0.227	–0.6	0.208	–1.6	0.078	0.8	0.812
3	2003	—	—	—	—	—	—	–1.5	0.080
	2004	—	—	—	—	—	—	–1.8	0.059
	2005	–1.7	0.066	0.6	0.664	–0.8	0.172	–2.1	0.039
	2006	–2.0	0.044	–0.9	0.156	–0.7	0.203	–1.9	0.049
4	2003	—	—	—	—	—	—	–6.0	0.001*
	2004	—	—	—	—	—	—	–1.5	0.079
	2005	–2.3	0.030*	0.5	0.619	–0.4	0.293	–4.0	0.005*
	2006	–11.1	<0.001*	–1.4	0.096	–9.4	<0.001*	–12.1	<0.001*
5	2004	—	—	–1.9	0.056	—	—	—	—
6	2004	–2.8	0.014*	0.4	0.554	–3.7	0.005*	–2.6	0.019*
	2005	0.3	0.557	1.0	0.933	0.3	0.576	–0.6	0.214
	2006	–1.9	0.049	–0.5	0.246	–1.0	0.143	–2.1	0.043
10	2005	—	—	–1.2	0.114	—	—	—	—

* Indicates a significant relationship at $\alpha = 0.033$ (0.10/3); P-values are listed in parentheses.

Table 1.8. Mean home-range size (MCP) for male (adults only) and female (adults and subadults) black bears combined for localities in the western U.S.

Author	Location	Home-range size (km^2) male	Home-range size (km^2) female
This study	**Rocky Mountain National Park, Colorado**	**103.0**	**47.3**
Costello et al. 2001	northern New Mexico	132.1	24.0
Costello et al. 2001	westcentral New Mexico	130.1	43.1
Beck 1991	westcentral Colorado	112.6	30.3
Bates 1991	central Utah	112.7	39.3
Novick and Stewart 1982	San Bernardino Mts, California	24.7	16.1
Goodrich 1990	Sierra Nevada Mountains, Nevada	36.9	16.5
Goodrich 1990	Sweetwater Mountains, Nevada	133.3	52.2
Amstrup and Beecham 1976, Reynolds and Beecham 1980	Middle Fork Weiser River, Idaho	77.7	26.4
Wertz et al. 2001, Wertz personal communication	northeastern Oregon	162.6	37.0
Rohlman 1989	Priest Lake, Idaho	34.6	10.9
Kasworm and Manley 1988	Cabinet Mts, Montana	76.9	17.4
Rosgaard and Simmons 1982, Greer 1987 Mack 1988	southcentral Montana	162.4	23.6
Aune 1994	northwestern Montana	224.8	137.3
	$\bar{x}$:	109.3	28.0[a]
	95% CI:	74.2–144.5	20.1–36.1[a]

[a] Excludes data from Aune 1994 due to extreme outlier.

in smaller home-ranges of female black bears in RMNP, presumably due to greater forage productivity (Koehler and Pierce 2003).

Contemporary adult male home-ranges ($\bar{x}$ = 77.9 km^2) were larger than historic values for RMNP ($\bar{x}$ = 35.6 km^2; Zeigenfuss 2001). Reasons for this increase in home-range size are difficult to explain but may be related to low sample size and inclusion of sub-adults in the estimated values from historic data (Zeigenfuss 2001). I obtained sufficient locations for home-range size of only 1 subadult male; this home-range was substantially smaller (8.7 km^2) than that of adults. Unlike females, the average size of adult male home-ranges in RMNP fell within the 95% CI of the pooled mean of other western U.S black bear populations, indicating that sizes of adult male home-ranges in RMNP were similar to other western U.S. populations (Table 8).

The size of male and female home-ranges did not vary significantly across seasons, although female home-range size tended to increase from spring to autumn. Seasonal home-ranges can fluctuate depending on reproductive access and forage availability (Alt et al. 1980, Rogers 1987, Beck 1991, Schwartz and Franzmann 1991, Samson and Huot 1998). These factors appeared to have less influence on black bears in RMNP, perhaps due to already large annual and seasonal female home-ranges. Climatic factors also exerted little influence on spring, summer, and autumn home-range sizes independently, but a positive relationship was observed with MaxTemp when averaged across seasons. This similarity with annual home-range size was not unexpected given the similarity in home-range size across seasons and relationships of MaxTemp to annual home-range size.

The degree of overlap of female home-ranges can be quite variable, with some studies showing extensive home-range overlap (e.g., Lindzey and Meslow 1977, Reynolds and Beecham 1980, Beck 1991, Wooding and Hardisky 1994, Hirsch et al. 1999) while others show little

(Jonkel and Cowan 1971, Rogers 1987, McCutchen 1990). Two primary factors have been implicated in affecting the degree of home-range overlap in female black bears, genetic relatedness (Jonkel and Cowan 1971, Lindzey and Meslow 1977, Rogers 1987) and habitat quality (Reynolds and Beecham 1980, Garshelis and Pelton 1981, Rogers 1987, McLoughlin et al. 2000, Oli et al. 2002). Several authors have suggested that genetically related females often show greater home-range overlap than non-related females (e.g., Lindzey and Meslow 1977, Pelchat and Ruff 1986, Rogers 1987, Oli et al. 2002). However, Schenk et al. (1998) found that females were not directly related to other females with overlapping home-ranges; McLoughlin et al. (2000) found similar results for brown bears (*Ursus arctos*). In RMNP, the amount of overlap was high for a mother and juvenile daughter in the 1st year following capture (71%), but decreased substantially in subsequent years (26%). Therefore, although related females in some regions may share portions of overlapping home-ranges, factors other than relatedness also influence this relationship.

A more likely factor influencing degree of female home-range overlap was forage availability. Results from a study of 30 brown bear populations indicated that extensive home-range overlap occurred in areas with abundant and limited food sources, while more intermediate areas had less overlap (McLoughlin et al. 2000). In RMNP, McCutchen (1990) reported little overlap for female black bears, but this was based on only 2 individuals. In contrast, I found that overlap of female home-ranges varied substantially across years (Tables 3 and 5), with less overlap in cooler, wetter years. Combined with smaller home-ranges during cooler, wetter years, this further suggests that habitat quality was higher during cooler, wetter years and poorer in hot, dry years in RMNP, given the effects of temperature and precipitation on plant productivity in Rocky Mountain forest types (Beidleman et al. 2000).

Seasonal home-ranges showed less overlap among females than did annual home-ranges, suggesting temporal segregation of use by females. The amount of overlap was particularly minimal during spring (Table 5). In North Carolina, home-range overlap was greatest in summer, with no significant difference detected between spring and autumn (Horner and Powell 1990). No difference in home-range overlap was reported during pre- and post-mast seasons in western Colorado (Beck 1991), with similar results noted in Arkansas (Oli et al. 2002). This seasonal variability may again be related to food abundance, as home-range overlap is generally greatest in areas where resources are patchy or limiting (Amstrup and Beecham 1976, McLoughlin et al. 2000, Samson and Huot 2001). Spring diets of black bears in RMNP included non-patchy food items (i.e., herbaceous material and insects; see Chapter 6 and Zeigenfuss 2001); more uniform distribution of food sources should reduce overlap. Although no climatic factors were related to female home-range overlap for each specific season, collectively, they again reflected less overlap during cooler, wetter years when plant growth would be greater (Beidleman et al. 2000).

Further, the levels of overlap I observed in RMNP were minimal values, as other uncollared females were possibly present and may have overlapped home-ranges of radiocollared females. Not accounting for all potential overlap may have reduced my ability to detect differences for individual seasons. Social instability may also have influenced the amount of overlap, as 1 RMNP female was harvested in 2005. The removal of this female likely reduced overlap values for 2006 and may have resulted in a shift in other female home-ranges. Such a situation was noted in Manitoba, Canada (Klenner 1987), and reflects the dynamic interaction between black bear movements and habitat use.

The distribution of locations of females varied considerably across years, with annual shifts most common during autumn (Table 6). Likewise, shifts in locations within years were most pronounced between summer and autumn seasons (Table 7). This seasonal shift coincided with soft mast production (i.e., huckleberry [*Vaccinium* spp.], raspberry [*Rubus* spp.], chokecherry [*Prunus virginiana*]); the patchiness of these resources likely resulted in greater movements because of high annual variation in production of these foods driven by high annual variability in climatic and other environmental factors (Rogers 1976, Samson and Huot 2001). In RMNP, changes in MaxTemp and Precip were associated with distributional shifts of female black bears during autumn, which is the most important season for fat accretion in black bears (Pelton 2003). Black bears likely seek out whatever resources are available given the temperature and precipitation regimes of a particular year. Because resource availability varied both spatially and temporally in RMNP (see Chapter 7), female black bear distributions likely shifted as resource availability changed. Female black bears responded more to altered resource availability through distributional shifts rather than through the size or composition of autumn home-ranges. Because home-range sizes decreased as surrogates for plant productivity increased in RMNP, these shifts were likely related to movements to areas of highest resource availability, with bears then remaining localized in these areas during years with abundant resources (cool, wet = smaller annual home-ranges) and doing significantly more searching during years of low resource availability (hot, dry = larger annual home-ranges).

MANAGEMENT IMPLICATIONS

Climatic factors that correlate with plant productivity were frequently related to numerous aspects of black bear distributions in RMNP. These interactions suggested the importance of food abundance on black bear distributions and home-range overlap. Habitat quality for black bears was higher during wetter years and lower during hot, dry years in RMNP, likely because of increased plant productivity. Black bear population densities are typically maintained at levels that are sustainable through frequent years of scarce food (Rogers 1976); thus, the carrying capacity of black bears in RMNP will likely be set at levels supportable during hot, dry years. Additionally, changes in movements and distributions associated with annual and seasonal variation in food abundance and distribution can lead to increased vulnerability to harvest and other mortality factors (Samson and Huot 1998). Although RMNP provides refuge from hunting, such protection is not always present once black bears cross the Park boundary. Harvesting resulted in 2 mortalities during my study and 2 additional mortalities during 1984–1991 (Zeigenfuss 2001). Although harvest was the proximate cause of these mortalities, lack of sufficient habitat may have been the ultimate cause. Lack of disturbances such as fire has allowed habitats to progress toward climax conditions with fewer early successional habitats present and an associated lack of edge and hence overall landscape patchiness in RMNP (McCutchen 1993, Bender and Keller 2005). The result is fewer areas favored by black bears for foraging and a landscape mosaic in RMNP that does not provide the diversity or fractal pattern preferred by black bears in RMNP (see Chapter 7). Possible negative consequences of this include increased use of human-related habitats by black bears in RMNP (see Chapters 2, 5, and 7). Because black bear numbers are low in RMNP, actions that potentially limit black bear mortality, such as increasing foraging areas in RMNP, can help sustain RMNP's black bear population. However, precipitation and plant productivity will still likely be the principal limiting factor for black bears in RMNP.

LITERATURE CITED

Alt, G. L., G. J. Matula, Jr., F. W. Alt, and J. S. Lindzey. 1980. Dynamics of home range and movements of adult black bears in northeastern Pennsylvania. International Conference on Bear Research and Management 4:131–136.

Amstrup, S. C., and J. Beecham. 1976. Activity patterns of radio-collared black bears in Idaho. Journal of Wildlife Management 40:340–348.

Aune, K. E. 1994. Comparative ecology of black and grizzly bears on the Rocky Mountain Front, Montana. International Conference on Bear Research and Management 9:365–374.

Bates, S. B. 1991. Home range, habitat selection, and food habits of central Utah black bears. Thesis, Brigham Young University, Provo, Utah, USA.

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

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

Bender, L. C., and B. J. Keller. 2005. Behavioral implications of bighorn sheep (*Ovis canadensis canadensis*) use of the Sheep Lakes mineral site, Rocky Mountain National Park, Colorado. Final Report, U.S. National Park Service—Rocky Mountain National Park, Estes Park, Colorado, USA.

Berry, K. J., and P. W. Mielke. 1983. Computation of finite population parameters and approximate probability values for multi-response permutation procedures (MRPP). Communications in Statistics—Simulation and Computation 12:83–107.

Bunnell, F. L., and D. E. N. Tait. 1981. Population dynamics of bears—implications. Pages 75–98 *in* C. W. Fowler and T. D. Smith, editors. Dynamics of large mammal populations. John Wiley and Sons, Inc., New York, USA.

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, New Mexico, USA.

DeYoung, R. W., E. C. Hellgren, T. E. Fulbright, W. F. Robbins, and I. D. Humphreys. 2000. Modeling nutritional carrying capacity for translocated desert bighorn sheep in western Texas. Restoration Ecology 8:57–65.

Garshelis, D. L., and M. R. Pelton. 1981. Movements of black bears in the Great Smoky Mountains National Park. Journal of Wildlife Management 45:912–925.

Goodrich, J. M. 1990. Ecology, conservation and management of two western Great Basin black bear populations. Thesis, University of Nevada Reno, Reno, Nevada, USA.

Greer, S. Q. 1987. Home range, habitat use, and food habits of black bears in south-central Montana. Thesis, Montana State University, Bozeman, Montana, USA.

Hirsch, J. G., L. C. Bender, and J. B. Haufler. 1999. Black bear, *Ursus americanus,* movements and home ranges on Drummond Island, Michigan. Canadian Field-Naturalist 113:221–225.

Horner, M. A., and R. A. Powell. 1990. Internal structure of home ranges of black bears and analyses of home range overlap. Journal of Mammalogy 71:402–410.

Hosmer, D. W., and S. Lemeshow. 2000. Applied logistic regression. John Wiley and Sons, New York, New York, USA.

Jonkel, C. J., and I. McT. Cowan. 1971. The black bear in the spruce-fir forest. Wildlife Monographs 27.

Kasworm, W. F., and T. Manley. 1988. Grizzly bear and black bear ecology in the Cabinet Mountains of Northwest Montana. Montana Department of Fish, Wildlife, and Parks, Helena, Montana, USA.

Klenner, W. 1987. Seasonal movements and home range utilization patterns of the black bear, *Ursus americanus*, in western Manitoba. Canadian Field-Naturalist 101:558–568.

Koehler, G. M., and D. J. Pierce. 2003. Black bear home-range sizes in Washington: climatic, vegetative, and social influences. Journal of Mammalogy 84:81–91.

Lindzey, F. G., and E. C. Meslow. 1977. Home range and habitat use by black bears in southwestern Washington. Journal of Wildlife Management 41:413–425.

Mack, J. A. 1988. Ecology of black bears on the Beartooth face, south-central Montana. Thesis, Montana State University, Bozeman, Montana, USA.

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.

McCutchen, H. E. 1993. Ecology of high mountain black bear population in relation to land use at Rocky Mountain NP. Park Science 13:25–27.

McLoughlin, P. D., S. H. Ferguson, and F. Messier. 2000. Intraspecific variation in home range overlap with habitat quality: a comparison among brown bear populations. Evolutionary Ecology 14:39–60.

Mohr, C. O. 1947. Table of equivalent populations of North American small mammals. American Midland Naturalist 37:223–249.

Novick, H. J., and G. R. Stewart. 1982. Home range and habitat preferences of black bears in the San Bernardino Mountains of southern California. California Fish and Game 67:21–35.

Oli, M. K., H. A. Jacobson, and B. D. Leopold. 2002. Pattern of space use by female black bears in the White River National Wildlife Refuge, Arkansas, USA. Journal for Nature Conservation 10:87–93.

Pelchat, B. O., and R. L. Ruff. 1986. Habitat and spatial relationships of black bears in boreal mixedwood forest of Alberta. International Conference on Bear Research and Management 6:81–92.

Pelton, M. R. 2000. Black bear. Pages 389–408 *in* S. Demarais and P. R. Krausman, editors. Ecology and management of large mammals in North America. Prentice-Hall, Upper Saddle River, New Jersey, USA.

Pelton, M. R. 2003. Black bear (*Ursus americanus*). Pages 547–555 *in* G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, editors. Wild mammals of North America: biology, management, and conservation. Second edition, revised. The Johns Hopkins University Press, Baltimore, Maryland, USA.

Polis, G. A., S. D. Hurd, C. T. Jackson, and F. S. Piñero. 1997. El Niño effects on the dynamics and control of an island ecosystem in the Gulf of California. Ecology 78:1884–1897.

Powell, R. A. 2000. Animal home ranges and territories and home range estimators. Pages 65–110 *in* L. Boitani and T. K. Fuller, editors. Research techniques in animal ecology. Columbia University Press, New York, New York, USA.

Powell, R. A., J. W. Zimmerman, and D. E. Seaman. 1997. Ecology and behavior of North American black bears: home ranges, habitat and social organization. Chapman and Hall, London, United Kingdom.

Reynolds, D. G., and J. J. Beecham. 1980. Home range activities and reproduction of black bears in west-central Idaho. International Conference of Bear Research and Management 4:181–190.

Rogers, L. L. 1976. Effects of mast and berry crop failures on survival, growth, and reproductive success of black bears. Transactions of the North American Wildlife and Natural Resource Conference 41:431–438.

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.

Rohlman, J. A. 1989. Black bear ecology near Priest Lake, Idaho. Thesis, University of Idaho, Moscow, Idaho, USA.

Rosgaard, A., and C. Simmons. 1982. East Boulder big game technical report. Montana Department of Fish, Wildlife and Parks, Helena, Montana, USA.

Samson, C., and J. Huot. 1998. Movements of female black bears in relation to landscape vegetation type in southern Québec. Journal of Wildlife Management 62:718–727.

Samson, C., and J. Huot. 2001. Spatial and temporal interactions between female American black bears in mixed forests of eastern Canada. Canadian Journal of Zoology 79:633–641.

Schenk, A., M. E. Obbard, and K. M. Kovacs. 1998. Genetic relatedness and home-range overlap among female black bears (*Ursus americanus*) in northern Ontario, Canada. Canadian Journal of Zoology 76:1511–1519.

Schwartz, C. C., and A. W. Franzmann. 1991. Interrelationship of black bears to moose and forest succession in the northern coniferous forest. Wildlife Monographs 113.

Seaman, D. E., J. J. Millspaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke, and R. A. Gitzen. 1999. Effects of sample size on kernel home range estimates. Journal of Wildlife Management 63:739–747.

Slauson, W. L., B. S. Cade and J. D. Richards. 1991. Users manual for BLOSSOM statistical software. United States Fish and Wildlife Service, National Ecology Research Center, Fort Collins, Colorado, USA.

Wertz, T. L., J. J. Akenson, M. G. Henjum, and E. L. Bull. 2001. Home range and dispersal patterns of subadult black bears in northeastern Oregon. Western Black Bear Workshop 7:93–100.

White, G. C., and R. A. Garrott. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, California, USA.

Wooding, J. B., and T. S. Hardisky. 1994. Home range, habitat use, and mortality of black bears in north-central Florida. International Conference on Bear Research and Management 9:349–356.

Worton, B. J. 1995. Using monte carlo simulation to evaluate kernel-based home range estimators. Journal of Wildlife Management 59:794–800.

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

Zeigenfuss, L. C. 2001. Ecology of black bears in Rocky Mountain National Park: an analysis of population dynamics, diet, and habitat selection (1985–1991). Unpublished report, U.S. National Park Service, Rocky Mountain National Park, Colorado, USA.

Chapter 2:

Trends in body condition and body weights of black bears in Rocky Mountain National Park, Colorado

Roger A. Baldwin, Department of Animal and Range Sciences, New Mexico State University, P.O. Box 30003 MSC 4901, Las Cruces, New Mexico 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, New Mexico 88003, USA

Chapter summary: Knowledge of body condition is important in predicting health and performance of large mammal populations. Previous work in Rocky Mountain National Park (RMNP), Colorado, reported some of the lightest weights ever recorded for black bears (*Ursus americanus*) in North America, although more direct measures of body condition were not examined. We compared condition data collected from 2003–2006 with historic data (1984–1991) to assess trends in condition and weights over the last 15–20 years. We determined percent body fat (BF) and a body condition index (BCI) for 14 black bears in RMNP. Regression analysis indicated a tight relationship between these condition indices ($R^2 = 0.962$). We estimated BF and BCI for additional black bears in RMNP using weight and BF regression equations. We developed separate equations predictive of weight (kg) for males and females based on girth measurements (cm) to estimate missing weights in our data set and to provide a future management tool for RMNP staff. BCI and BF increased in females over the last 15–20 years; similar values for males were not significant, though small sample sizes limited power. Comparisons of weights indicated a substantial size increase within certain sex and age classes from historic data in RMNP, and contemporary weights were consistent with those reported for other western U.S. localities. Weight models were compared to those derived for other populations and indicated that weight-morphology relationships were more consistent within specified elevation zones. Black bear size and condition increased in RMNP since the 1980's, with increased use of anthropogenic habitats and food sources likely responsible for this change.

An accurate assessment of body condition is a key step toward understanding fundamental aspects of animal ecology (i.e., habitat use, food habits, reproduction, survival; Hanks 1981, Franzmann 1985, Rogers 1987, Gaillard et al. 2000, Bender and Cook 2005, Bender et al. 2007a, b, c; Lomas and Bender 2007). Although body weight has often been related to black bear (*Ursus americanus*) demographics and habitat use (Noyce and Garshelis 1994, Samson and Huot 1995), it is not a direct measure of body condition (Farley and Robbins 1994, Chan-McLeod et al. 1995, Gau and Case 1999) and may be a poor indicator of condition (Cook et al. 2001). More exact measures of body condition that directly measure body fat (BF) and muscle reserves (e.g., bioelectrical impedance analysis [BIA], body condition index [BCI]) have been developed and have proven effective at estimating condition in black bears. The advent of BIA procedures has allowed for rapid (5–15 minutes; Noyce et al. 2002) and accurate (R^2 = 0.96, SEE = 2.2% [Farley and Robbins 1994]; R^2 = 0.88, SEE = 3.3% [Hilderbrand et al. 1998]) assessments of BF levels in black bears which can be related to dietary, habitat, and population demographic information to provide a more accurate interpretation of these factors. However, BIA equipment is costly, requires careful handling, and is sensitive to factors such as body position, stomach content, and user training (Farley and Robbins 1994, Hilderbrand et al. 1998).

The BCI is another effective method for assessing condition of individuals that is much less costly, less sensitive to stomach content (though such content will still influence weight values), and requires only basic training (Cattet et al. 2002). BCI values reflect the combined mass of BF and lean muscle tissue of an individual relative to its body size (Cattet et al. 2002). Investigations that assess body condition solely on the amount of BF present on an animal (e.g., Stephenson et al. 1998, Gau and Case 1999) may underestimate condition because lean body mass can be a significant source of energy for black bears when BF reserves are low or exhausted (Atkinson et al. 1996, Hilderbrand et al. 2000). BCI values account for this additional source of energy which represents an important consideration in condition assessments, as a change in mass of BF is usually paralleled by a change in muscle mass (Ryg et al. 1990, Atkinson et al. 1996). However, interpretation of this index is less intuitive than estimated BF levels. A close relationship between these condition indices could allow for rapid and efficient conversion between these estimates.

Studies of black bears have often used weight as a surrogate for condition (e.g., Rogers 1987, Hellgren et al. 1989, Samson and Huot 1995), and knowledge of weights is thus often useful for comparisons with previous studies. However, weights can be difficult to obtain in a field setting (Cattet et al. 1997). Equations that predict weight from simple body measurements have been developed for many black bear populations (Payne 1976, Swenson et al. 1987, Cattet 1990) but vary substantially among populations (Cattet et al. 1997). Swenson et al. (1987) provided evidence that predictions might be improved by relating equations across similar elevational zones, while Cattet (1990) suggested that an increase in the number of variables representative of size would better describe the relationship between morphological measurements and weight. Nonetheless, predictions for local populations typically yield the most accurate results (Swenson et al. 1987, Cattet et al. 1997).

Previous work in Rocky Mountain National Park (RMNP), Colorado, did not assess black bear condition, but found that black bear body weights were among the lightest recorded (McCutchen 1993, Zeigenfuss 2001). This small size was attributed to poor habitat and minimal food abundance (McCutchen 1993, Zeigenfuss 2001) and was hypothesized to be responsible for low recruitment and productivity rates of black bears in RMNP. However, mass alone may not adequately reflect true nutritional condition (Cook et al. 2001), and it is body condition, not mass per se, that is the fundamental driver of survival and productivity in large mammals (Hanks 1981, Cook et al. 2001, Noyce et al. 2002, Lomas and Bender 2007, Bender et al. 2007a, b). Because of historically low productivity and small size of black bears in RMNP, my goal was to rigorously assess body condition of black bears in RMNP to see whether condition was low relative to other populations of black bears in North America. My objectives were to: 1) determine nutritional condition of black bears in RMNP in the contemporary period; 2) derive equations predictive of BF levels from BCI scores to assess historical levels of condition of black bears in RMNP; and 3) compare BF and BCI scores between contemporary and historic data in RMNP to determine any change in condition over time. Because of the use of mass in BCI scores, further objectives included: 4) deriving local equations to predict weight of black bears in RMNP; 5) compare predicted weights to predictions from models built from other populations to determine relationships between estimated weights and elevational zones and model parameters; and 6) compare weights of black bears in RMNP to other black bear populations throughout the western U.S. to see if differences exist among populations.

METHODS

I captured black bears using modified Aldrich foot snares, culvert traps, and wire-cage traps from 1984–1991 (hereafter, historic) and 2003–2006 (hereafter, contemporary), and den sites of collared black bears were also visited from 2003–2006. I immobilized black bears with a 5:1 mixture of ketamine hydrochloride and xylazine hydrochloride (200 mg ketamine and 40 mg xylazine per ml). Once immobilized, I fit individuals with radiocollars and classed bears into appropriate sex and age categories (subadult vs. adult); adult females were differentiated from subadults based on known age, nipple size, and nipple coloration (Beck 1991, Brooks and McRoberts 1997), while adult males were designated by larger size, obvious staining of teeth, and descended testicles (Beck 1991, Garshelis and Hellgren 1994). I also collected morphometric data including dorsal contour length (DCL), straight-line body length (SLBL), girth, and weight. For DCL (cm), I measured 2 lengths following the contour of the backbone: 1) from the tip of the nose to the base of the tail, and 2) from the tip of the nose to the last tail vertebrae. I used measurements to the base of the tail in BF estimation, while those to the tip of the last tail vertebrae were used for weight estimation. I recorded SLBL (cm) as the measure of the straight line distance from the tip of the nose to the end of the last tail vertebra as determined with a measuring tape suspended above the individual while in sternal recumbency (Cattet et al. 2002). For girth (cm), I measured the circumference of the chest immediately behind the front legs with lungs in deflated position (Beck 1991). I weighed black bears using a spring scale to the nearest kg. I recorded these same measurements during early (October–December) and late (March–April) denning periods (hereafter referred to as winter and spring, respectively) to track fluctuations throughout the year.

Because SLBL was not measured for the 1984–1991 period, I regressed girth and DCL measurements to known weights to allow prediction of unknown weights for historic and contemporary data. I also regressed DCL (including tail measurement) to known SLBL measurements to allow estimation of SLBL for historic data, as these measures were included in BCI scores (Cattet et al. 2002). I separated data by sex for weight estimation given occasional differences between males and females in modeled relationships (Swenson et al. 1987), though such separation was not warranted for SLBL estimation. I plotted regression residuals to determine outliers and selected models based on R^2 values (Ramsey and Schafer 1997). I then compared differences (absolute values) in actual weights of black bears in RMNP to (1) estimated weights from the model derived for RMNP, (2) estimated weights derived from models of a high elevation population in Montana (Swenson et al. 1987), and (3) estimated weights derived from a prediction model developed in Alberta, Canada (Cattet 1990). The study in Montana provided equations for each sex separately; the equation for females included girth and body index (= $\text{girth}^2 \times \text{DCL}$) and was a composite of equations derived from 3 different sample locations, whereas the equation for males included only girth. Models constructed in

Alberta included girth, SLBL, and age of individual. I compared differences between known weights and estimates using 1-way ANOVA and LSD multiple comparisons test with an experiment-wise error rate of $\alpha = 0.05$. These comparisons allowed us to ascertain the similarity between estimates for similar elevational zones (Montana, Swenson et al. 1987) and to assess whether models including additional metrics (Alberta, Cattet 1990) were better able to predict weights from a variety of locations. Finally, I related historic and contemporary weights in RMNP to other western U.S. localities to asses the size of black bears in RMNP relative to other populations.

I used BIA to assess BF in black bears during den checks and some capture events. This technique measured the resistance of an electrical current that was passed through the bear and related this resistance measurement to DCL (excluding tail measurement) and weight to estimate BF (Farley and Robbins 1994, Hilderbrand et al. 1998). To determine resistance, I used a Quantum II (RJL Systems, Detroit, Michigan, USA) analyzer that was comparable to the Model 101A used in other black bear studies (e.g., Farley and Robbins 1994, Atkinson and Ramsay 1995, Hilderbrand et al. 1998, 2000). For resistance measurements, I placed bears in a sternally recumbent position with hind legs extended backward and front legs extended forward parallel to the length of the body (Gau and Case 1999, 2002). I placed bears on a plastic tarp to eliminate conductivity problems associated with ground moisture (Farley and Robbins 1994, Atkinson and Ramsay 1995). I positioned electrodes in a snout to tail configuration with alligator clamps attached to the lips and needle electrodes inserted 3 cm to either side of the base of the tail (Farley and Robbins 1994). Measurements were taken multiple times to verify readings.

Additionally, I obtained BCI scores for black bears using SLBL and weight (Cattet et al. 2002). BCI values are strongly correlated to true body condition ($r = 1.0$, $P < 0.001$; Cattet et al.

2002) and reflect the combined mass of BF and skeletal muscle of an individual relative to its body size. I regressed BCI scores and BF to model the relationship between these measures to predict BF for bears with only BCI scores and assessed residual plots for outliers (Ramsey and Schafer 1997). Only BF and BCI scores from directly measured weights, DCL, and SLBL were used in this regression. However, I also calculated BCI scores from estimated weights and SLBL for comparative purposes between historic and contemporary black bear data. I then used those BCI scores to estimate BF using the modeled relationship. I acknowledge the compounded error associated with such an approach (Cattet 1990) and consequently were conservative in interpretation of results. Finally, I compared BCI and BF between contemporary and historic RMNP black bear data during the summer season using Mann–Whitney *U*-tests; I combined adult and subadult age classes to increase sample sizes. I also calculated mean values for winter and spring, although comparisons with historic data for these seasons were not possible as similar data were not available from 1984–1991.

RESULTS

I was able to relate BCI to BF from 6 capture events and 8 den checks. Percent body fat was strongly related to BCI ($F_{1,14} = 141$, $P < 0.001$, $R^2 = 0.962$) which allowed for accurate prediction of BF from BCI scores: $\text{BF} = 7.070 + (8.915 \times \text{BCI}\ [\text{SE} = 1.250]) + (1.823 \times \text{BCI}^2\ [\text{SE} = 0.649])$ (Fig. 1). Additionally, I was able to predict SLBL from DCL ($F_{1,18} = 150$, $P < 0.001$, $R^2 = 0.903$; $\text{SLBL} = 17.304 + (0.774 \times \text{DCL}\ [\text{SE} = 0.063])$) and I used the resultant model to estimate BCI for historic bear data. BCI scores of adult females in summer were higher for the contemporary period ($U = 17.0$, $P = 0.080$), whereas BF did not differ ($U = 21.0$, $P = 0.172$;

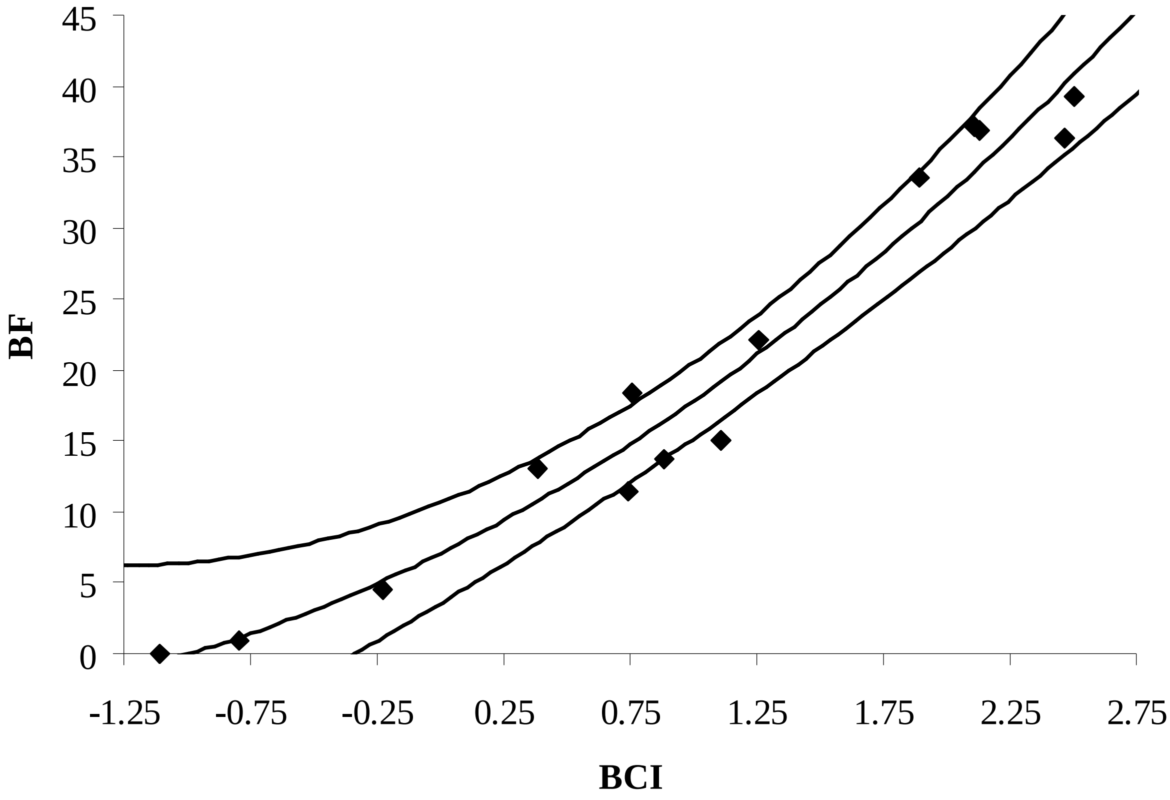

Figure 2.1. Relationship between body condition index (BCI) and percent body fat (BF) of black bears in Rocky Mountain National Park, Colorado: $BF = 7.070 + (8.915 \times BCI\ [SE = 1.250]) + (1.823 \times BCI^2\ [SE = 0.649])$, $R^2 = 0.962$. Also shown are 99% confidence bands.

Table 1). Neither BF (U = 36.0, P = 0.730) nor BCI (U = 31.0, P = 0.882) differed for males between periods (Table 1).

For the contemporary period, BF (U = 14.0, P = 0.105) and BCI (U = 16.0, P = 0.165) did not differ statistically for females during winter (BF: $\bar{x}$ = 32.7, SE = 3.8, n = 8; BCI: $\bar{x}$ = 2.113, SE = 0.322, n = 8) as compared to summer (BF: $\bar{x}$ = 22.8, SE = 4.9, n = 7; BCI: $\bar{x}$ = 1.312, SE = 0.349, n = 7); however, this was influenced strongly by 1 subadult in poor condition during winter (BF = 11.4, BCI = 0.742). Removal of this bear resulted in condition indices being significantly higher in winter than summer (BF: U = 8.0, P = 0.035; BCI: U = 10.0, P = 0.064). Following hibernation, BCI levels of females in spring ($\bar{x}$ = 0.657, SE = 0.137, n = 3) were lower than summer (U = 18.0, P = 0.087), though BF ($\bar{x}$ = 15.7, SE = 1.5, n = 3) did not differ (U = 15.0, P = 0.305). Winter (BF = 33.0, BCI = 2.035) and spring data (BF = 18.2, BCI = 1.032) were available for only 1 male.

I recorded weight, girth, and DCL ≥ 1 time for 23 black bears (11 female, 12 male) from 1984–1991 and 16 black bears (13 female, 3 male) from 2003–2006. The best predictive equation for black bear weight in RMNP included only girth for both males ($F_{1,15}$ = 325, P < 0.001, R^2 = 0.962; β = 1.720, SE = 0.095; Fig. 2a) and females ($F_{1,24}$ = 304, P < 0.001, R^2 = 0.933; β = 1.386, SE = 0.079; Fig. 2b). Absolute differences in predicted weights did not vary between equations derived for RMNP and Montana populations (males: P = 0.815; females: P = 0.139), but differed from equations derived in Alberta for both males (P = 0.004) and females (P = 0.011; Table 2).

Weights of males and females during summer were greater for both adult and subadult age classes in the contemporary period in RMNP as compared to historic data (Table 3). For the contemporary period, mean weights ($\bar{x}$ = 93.2, SE = 7.9, n = 8) of females in winter were higher

Table 2.1. Comparison between percent body fat (BF) and body condition index (BCI) in summer for black bears in Rocky Mountain National Park, Colorado during historic (1984–1991) and contemporary (2003–2006) sampling periods.

		BF			BCI		
Sex	Years	$\bar{x}$	SE	*n*	$\bar{x}$	SE	*n*
Female	1984–1991	15.0	2.4	10	0.715A[a]	0.198	10
	2003–2006	22.8	4.9	7	1.312B	0.349	7
Male	1984–1991	13.0	1.7	13	0.535	0.166	13
	2003–2006	12.0	5.1	5	0.365	0.551	5

[a] Differences (denoted by different letters) in mean values between sampling periods were tested for each sex using a Mann–Whitney *U* comparison with significance set at $\alpha = 0.10$.

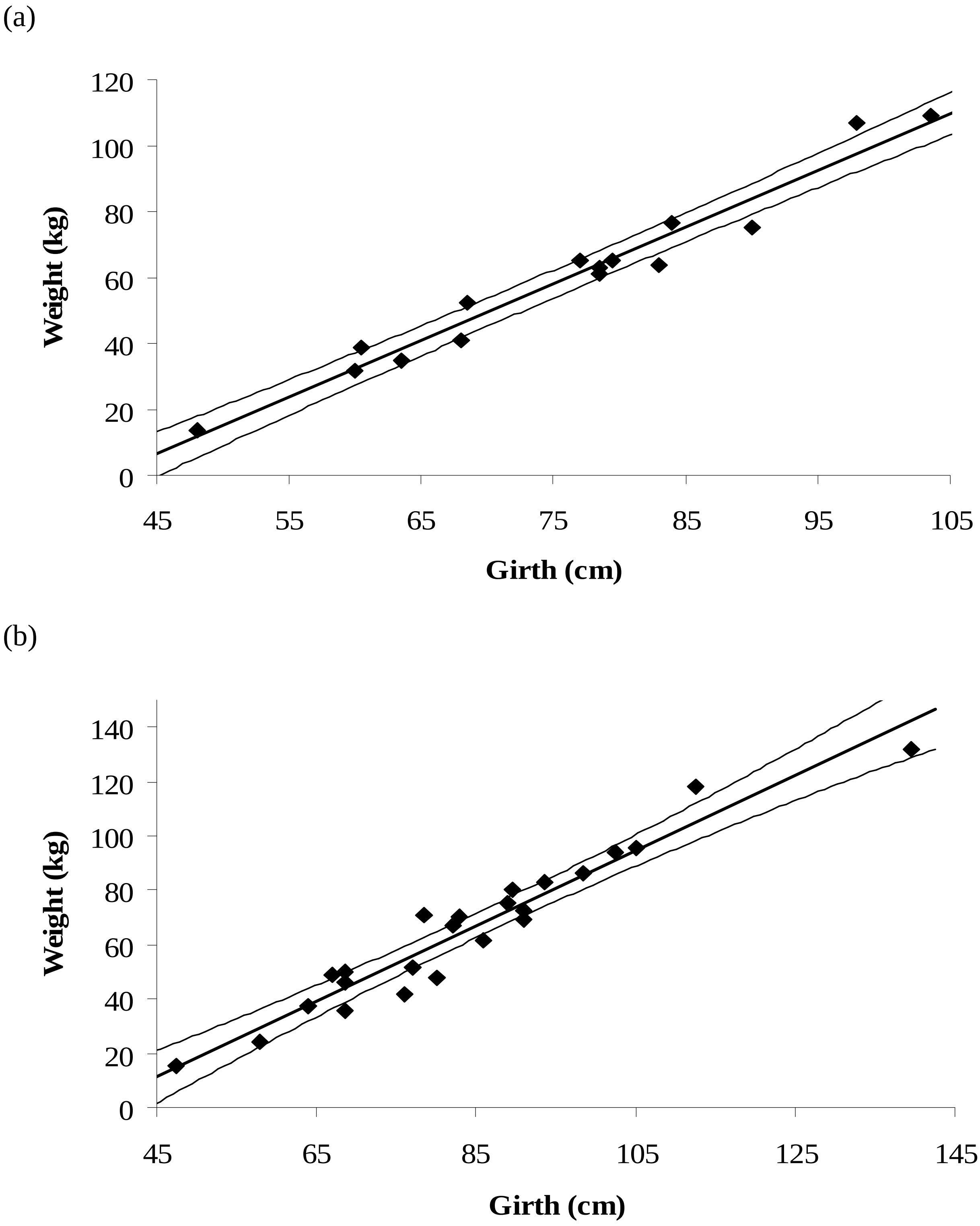

Figure 2.2. Relationships between girth and weight of male (a) and female (b) black bears in Rocky Mountain National Park, Colorado. Model equations: (a) weight = –71.034 + 1.720 (SE = 0.095) × girth—R^2 = 0.962, and (b) weight = –50.847 + 1.386 (SE = 0.079)—R^2 = 0.933. Also shown are 99% confidence bands.

Table 2.2. Mean difference (absolute value) between actual weights (kg) and estimated values derived from morphological measurements (cm) using different predictive equations for black bears in Rocky Mountain National Park (RMNP), Colorado.

	RMNP[a]			Montana[b]			Alberta[c]		
Sex	$\bar{x}$	SE	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE	*n*
Female	5.7A[d]	0.8	23	7.7AB	0.7	23	9.9B	1.9	14
Male	4.1A	0.7	15	4.5A	0.8	15	9.0B	1.9	11

[a] This study: weight = –50.847 + (1.386 × girth) for females; weight = –71.034 + (1.720 × girth) for males.

[b] From Swenson et al. (1987): weight = 0.631(8.978 + [0.0000579 × body index]) + 0.369(21.32 + [0.0000354 × body index]) for females; weight = $0.00191(\text{girth}^{2.377})$ for males. Body index = girth^2 × dorsal contour length.

[c] From Cattet (1990): weight = $e^{-8.16}(\text{girth}^{1.39})(\text{straight-line body length}^{1.21})(\text{age}^{0.08})$. Sexes were combined.

[d] Significant differences (LSD multiple comparisons test, $P < 0.05$) are illustrated by different letters following mean values for females and males.

Table 2.3. Comparison of contemporary (2003–2006) and historical (1984–1991) black bear weights (kg) by sex and age class and comparisons to mean values for other western U.S. localities.

	2003–2006[a]	1984–1991[a]	western U.S.
Adult male	99.2 (4)	74.2 (10)	101.2[b]
Adult female	67.6 (4)	59.8 (6)	62.6[b]
Subadult male	72.2 (2)	40.0 (4)	44.9[c]
Subadult female	48.1 (4)	39.8 (4)	34.0[c]

[a] numbers in parentheses indicate sample size.

[b] values derived from the following studies: Bates 1991, Beecham 1980, Beck 1991, Beckmann and Berger 2003b, Costello et al. 2001, Frost 1990, Goodrich 1990, Greer 1987, Jonkel and Cowan 1971, Kasworm and Manley 1988, Mack 1988, Piekielek and Burton 1975, Rohlman 1989, Rosgaard and Simmons 1982.

[c] values derived from the following studies: Bates 1991, Beck 1991, Costello et al. 2001, Frost 1990, Greer 1987, Jonkel and Cowan 1971, Kasworm and Manley 1988, Mack 1988, Piekielek and Burton 1975, Rohlman 1989, Rosgaard and Simmons 1982.

(U = 4.0, P = 0.003) than weights ($\bar{x}$ = 57.8, SE = 14.7, n = 8) during summer, while summer and spring ($\bar{x}$ = 59.5, SE = 12.4, n = 3) weights did not differ (U = 11.0, P = 0.838). I obtained winter (157.3 kg) and spring weights (137.1 kg) for only 1 male, and thus no comparisons were possible. Weights of black bears in RMNP during the contemporary period were similar to weights from other western localities (Table 3).

DISCUSSION

Female black bears in RMNP were in presumably good to excellent nutritional condition during summer 2003–2006 (BF = 22.8%; BCI = 1.312), based on comparisons with other captive and free-ranging black bear populations (see below). However, black bears in RMNP were in poorer condition historically (BF = 15.0%; BCI = 0.715). Differences between contemporary and historical condition were more pronounced for BCI values (82% increase for BCI, 52% increase for BF), thus indicating gains in both BF and muscle mass since the late 1980's. Results from spring sampling further reflected this pattern of increased condition, as condition levels at the end of hibernation from the contemporary population were essentially equivalent to those estimated in summer from historic data, even though BF stores should be lowest during early spring (Pelton 2003). Significantly, BF levels of females in winter in RMNP ($\bar{x}$ = 33%) were equivalent to values reported for a captive black bear population ($\bar{x}$ = 31%; Farley and Robbins 1995) and for 2 additional populations in Colorado and 1 in Wyoming ($\bar{x}$ = 32%; Harlow et al. 2002), indicating high nutritional condition for RMNP's black bear population.

Increases in condition of female black bears since the late 1980's suggests an increase in nutritional quality and/or quantity (Rogers 1987, Beckmann and Berger 2003a), though no major changes in vegetation composition are known to have occurred in RMNP during this period to explain this increase (Zeigenfuss 2001). This increase may be a response to greater use of anthropogenic food sources by RMNP's current black bear population, as such foods are much higher in calories, carbohydrates, proteins, and fats than most natural diets (Stringham 1989; see Chapter 6). Historically, black bears in RMNP exhibited cryptic behavior and were believed to avoid heavy human-use areas, at least east of the continental divide (McCutchen 1990; see Chapter 7). However, increased development along the boundary of RMNP has heightened the potential for human-bear encounters (Zeigenfuss 2001), and many black bears in the contemporary population no longer exhibit this avoidance of human-use areas (see Chapter 7). Further, BF and BCI in black bears was positively related to bear use of human-use areas in RMNP, especially during autumn (see Chapter 7).

In contrast to females, no increase in body condition was seen for males between historic and contemporary periods, though weights did differ. However, this lack of difference was strongly influenced by 2 males from the contemporary period that were in very poor condition at the time of capture (BF = 1.0% and 0.0%; BCI = –0.793 and –1.105). One of these individuals avoided human-use areas, while I was able to obtain only 3 locations for the other individual prior to censuring; I was not able to obtain condition data on these individuals at the peak of BF accretion in late autumn. Because the 1 male I obtained condition information for during winter and spring was in good condition (winter: BF = 33.0%, BCI = 2.035; spring: BF = 18.2%, BCI = 1.032), males may have exhibited similar increases in condition as females, but sample sizes were too small to adequately test this hypothesis.

Although weight has often been used as a surrogate for body condition, actual estimates of condition are more appropriate, though much harder to collect (Farley and Robbins 1994, Chan-McLeod et al. 1995, Gau and Case 1999). Body condition at the peak of seasonal accrual has been shown to be fundamental to virtually every survival and reproduction parameter of large mammals (Hanks 1981, Franzmann 1985, Rogers 1987, Gaillard et al. 2000, Bender and Cook 2005, Bender et al. 2007a, b, c; Lomas and Bender 2007), and should provide similar relationships for black bears. In particular, knowledge of body mass composition (i.e., BF and lean muscle mass) is more intuitive and preferred in some situations. For example, studies have examined changes in body composition between lactating and non-lactating black bears during hibernation to assess daily energy requirements and sources of these energy components (i.e., BF or protein; Farley and Robbins 1995, Harlow et al. 2002). This comparison would not be possible using just weights or BCI scores and underscores the need for rapid and accurate conversion of BCI scores to BF. Consequently, my model predicting BF from BCI should provide a useful tool for future research and management projects that require estimates of actual body condition.

Historical data from RMNP (McCutchen 1993, Zeigenfuss 2001) indicated lighter black bear weights than similar populations throughout the western U.S. (Table 3). This small size was attributed to poor habitat and low food abundance (McCutchen 1993, Zeigenfuss 2001). However, contemporary black bear weights are substantially greater than historic values and well within the range of those typically reported in other western U.S. localities (Table 3). The increase in body weights of black bears in RMNP is likely related to greater use of human-use areas and subsequent anthropogenic food sources (see Chapters 6 and 7) such as was previously observed near Lake Tahoe, Nevada, USA (Beckmann and Berger 2003a, b). Thus, the increase in black bear weights (and condition) may not indicate an increase in the quality of foraging habitat in RMNP. Rather, because black bears are using human sources of foods more than in the past (see Chapter 6), these high-energy foods (i.e., garbage and other human foods) may simply supplement natural diets, resulting in increased weights of bears (Stringham 1989).

Significant variability exists with equations for predicting mass of black bears (see Swenson et al. 1987 for review), and the hypothesis that use of a greater number of factors may explain much of this variation (e.g., Cattet 1990) was not supported in RMNP (Table 2), as girth alone proved effective in predicting weight of black bears. Girth is the measure most commonly associated with growth in black bears (Payne 1976, Alt 1980, Swenson et al. 1987), though models and model fit varies across populations. Comparing models of black bear weights among areas indicated that weights of black bears in RMNP differed from predictions of the Alberta model (Cattet 1990), while estimates from models developed in Montana (Swenson et al. 1987) were more representative of weights in RMNP. Therefore, I concur with Swenson et al. (1987) that elevational zones occupied by black bears likely significantly influences mass-morphology relationships. However, if local morphological models are available for predicting weight, they are more appropriate to use and provide the best information for future management practices, such as predicting BCI or BF.

MANAGEMENT IMPLICATIONS

Contemporary condition of black bears in RMNP is good to excellent, ostensibly suggesting that contemporary habitat conditions provide good foraging environments (but see Chapter 7). However, much of the increase in condition seen contemporarily versus historic levels was likely due to increased black bear use of human-wildland interface areas, indicating that bear condition may well reflect supplementation with human food sources rather than the quality of RMNP habitats as black bear foraging areas. In fact, a greater than 15 fold increase in consumption of anthropogenic foods has been noted during the contemporary period (see Chapter 6), and both BF and BCI of black bears is related to use of human-influenced habitats (see Chapter 7). This suggests high potential for increased negative bear-human encounters (Peirce and Van Daele 2006) which may threaten the viability of RMNP's black bear population. Increasing the quantity, quality, and distribution of high quality natural foods in RMNP may ameliorate this potential problem (see Chapter 7).

LITERATURE CITED

Alt, G. L. 1980. Rate of growth and size of Pennsylvania black bears. Pennsylvania Game News 51:7–17.

Atkinson, S. N., R. A. Nelson, and M. A. Ramsay. 1996. Changes in the body composition of fasting polar bears (*Ursus maritimus*): the effect of relative fatness on protein conservation. Physiological Zoology 69:304–306.

Atkinson, S. N., and M. A. Ramsay. 1995. Effects of prolonged fasting on the body composition and reproductive success of adult female polar bears (*Ursus maritimus*). Functional Ecology 9:559–567.

Bates, S. B. 1991. Home range, habitat selection, and food habits of central Utah black bears. Thesis, Brigham Young University, Provo, Utah, USA.

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

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

Beecham J. J. 1980. Population characteristics, denning, and growth patterns of black bears in Idaho. Dissertation, University of Montana, Missoula, Montana, USA.

Bender, L. C., and J. G. Cook. 2005. Nutritional condition of elk in Rocky Mountain National Park. Western North American Naturalist 65:329–334.

Bender, L. C., J. G. Cook, R. C. Cook, and P. B. Hall. 2007a. Relations between nutritional condition and survival of elk in the Pacific Northwest. Wildlife Biology 13: *In press*.

Bender, L. C., L. A. Lomas, and J. Browning. 2007b. Condition, survival, and cause-specific mortality of mule deer in northcentral New Mexico. Journal of Wildlife Management 71:1118–1124.

Bender, L. C., L. A. Lomas, and T. Kamienski. 2007c. Habitat effects on condition of doe mule deer in northcentral New Mexico. Rangeland Ecology and Management 60:277–284.

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.

Cattet, M. 1990. Predicting nutritional condition in black bears and polar bears on the basis of morphological and physiological measurements. Canadian Journal of Zoology 68:32–39.

Cattet, M. R. L., S. N. Atkinson, S. C. Polischuk, and M. A. Ramsay. 1997. Predicting body mass in polar bears: is morphometry useful? Journal of Wildlife Management 61:1083–1090.

Cattet, M. R. L., N. A. Caulkett, M. E. Obbard, and G. B. Stenhouse. 2002. A body-condition index for ursids. Canadian Journal of Zoology 80:1156–1161.

Chan-McLeod, A. C. A., R. G. White, and D. E. Russell. 1995. Body mass and composition indices for female barren-ground caribou. Journal of Wildlife Management 59:278–291.

Cook, R. C., J. G. Cook, D. L. Murray, P. Zager, B. K. Johnson, and M. W. Gratson. 2001. Nutritional condition models for elk: which are the most sensitive, accurate, and precise? Journal of Wildlife Management 65:988–997.

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, New Mexico, USA.

Farley, S. D., and C. T. Robbins. 1994. Development of two methods to estimate body composition of bears. Canadian Journal of Zoology 72:220–226.

Farley, S. D., and C. T. Robbins. 1995. Lactation, hibernation, and mass dynamics of American black bears and grizzly bears. Canadian Journal of Zoology 73:2216–2222.

Franzmann, A. W. 1985. Assessment of nutritional status. Pages 239–260 *in* R. J. Hudson and R. G. White, editors. Bioenergetics of wild herbivores. CRC Press, Boca Raton, Florida, USA.

Frost, H. C. 1990. Population and reproductive characteristics of black bears on an isolated mountain in southeastern Utah. Thesis, Brigham Young University, Provo, Utah, USA.

Gaillard, J.-M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toïgo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31:367–393.

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

Gau, R. J., and R. Case. 1999. Evaluating nutritional condition of grizzly bears via select blood parameters. Journal of Wildlife Management 63:286–291.

Gau, R. J., and R. Case. 2002. Evaluating nutritional condition of grizzly bears via ^{15}N signatures and insulin-like growth factor-1. Ursus 13:285–291.

Goodrich, J. M. 1990. Ecology, conservation and management of two western Great Basin black bear populations. Thesis, University of Nevada Reno, Reno, Nevada, USA.

Greer, S. Q. 1987. Home range, habitat use, and food habits of black bears in south-central Montana. Thesis, Montana State University, Bozeman, Montana, USA.

Hanks, J. 1981. Characterization of population condition. Pages 47–73 *in* C. W. Fowler and T. D. Smith, editors. Dynamics of large mammal populations. The Blackburn Press, Caldwell, New Jersey, USA.

Harlow, H. J., T. Lohuis, R. G. Grogan, and T. D. I. Beck. 2002. Body mass and lipid changes by hibernating reproductive and nonreproductive black bears (*Ursus americanus*). Journal of Mammalogy 83:1020–1025.

Hellgren, E. C., M. R. Vaughan, and R. L. Kirkpatrick. 1989. Seasonal patterns in physiology and nutrition of black bears in Great Dismal Swamp, Virginia-North Carolina. Canadian Journal of Zoology 67:1837–1850.

Hilderbrand, G. V., S. D. Farley, and C. T. Robbins. 1998. Predicting body condition of bears via two field methods. Journal of Wildlife Management 62:406–409.

Hilderbrand, G. V., C. C. Schwartz, C. T. Robbins, and T. A. Hanley. 2000. Effect of hibernation and reproductive status on body mass and condition of coastal brown bears. Journal of Wildlife Management 64:178–183.

Jonkel, C. J., and I. McT. Cowan. 1971. The black bear in the spruce-fir forest. Wildlife Monographs 27.

Kasworm, W. F., and T. Manley. 1988. Grizzly bear and black bear ecology in the Cabinet Mountains of Northwest Montana. Montana Department of Fish, Wildlife, and Parks, Helena, Montana, USA.

Lomas, L. A., and L. C. Bender. 2007. Survival and cause-specific mortality of neonatal mule deer fawns, north-central New Mexico. Journal of Wildlife Management 71:884–894.

Mack, J. A. 1988. Ecology of black bears on the Beartooth face, south-central Montana. Thesis, Montana State University, Bozeman, Montana, USA.

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.

McCutchen, H. E. 1993. Ecology of high mountain black bear population in relation to land use at Rocky Mountain NP. Park Science 13:25–27.

Noyce, K. V., and D. L. Garshelis. 1994. Body size and blood characteristics as indicators of condition and reproductive performance in black bears. International Conference on Bear Research and Management 9:481–496.

Noyce, K. V., P. L. Coy, and D. L. Garshelis. 2002. Bone prominence and skin-fold thickness as predictors of body fat and reproduction in American black bears. Ursus 13:275–284.

Payne, N. F. 1976. Estimating live weight of black bears from chest girth measurements. Journal of Wildlife Management 40:167–169.

Peirce, K. N., and L. J. Van Daele. 2006. Use of a garbage dump by brown bears in Dillingham, Alaska. Ursus 17:165–177.

Pelton, M. R. 2003. Black bear (*Ursus americanus*). Pages 547–555 *in* G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, editors. Wild mammals of North America: biology, management, and conservation. Second edition, revised. The Johns Hopkins University Press, Baltimore, Maryland, USA.

Piekielek, W., and T. S. Burton. 1975. A black bear population study in northern California. California Fish and Game 61:4–25.

Ramsey, F. L., and D. W. Schafer. 1997. The statistical sleuth: a course in methods of data analysis. Duxbury Press, Belmont, California, USA.

Rohlman, J. A. 1989. Black bear ecology near Priest Lake, Idaho. Thesis, University of Idaho, Moscow, Idaho, USA.

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.

Rosgaard, A., and C. Simmons. 1982. East Boulder big game technical report. Montana Department of Fish, Wildlife and Parks, Helena, Montana, USA.

Ryg, M., T. Smith, N. A. Øritsland. 1990. Seasonal changes in body mass and body composition of ringed seals (*Phoca hispida*) on Svalbard. Canadian Journal of Zoology 68:470–475.

Samson, C., and J. Huot. 1995. Reproductive biology of female black bears in relation to body mass in early winter. Journal of Mammalogy 76:68–77.

Stephenson, T. R., K. J. Hundertmark, C. C. Schwartz, and V. Van Ballenberghe. 1998. Predicting body fat and body mass in moose with ultrasonography. Canadian Journal of Zoology 76:717–722.

Stringham, S. F. 1989. Demographic consequences of bears eating garbage at dumps: an overview. Pages 35–42 *in* M. Bromley, editor. Bear–people conflicts—Proceedings of a symposium on management strategies. Northwest Territories Department of Renewable Resources, Yellowknife, Northwest Territories, Canada.

Swenson, J. E., W. F. Kasworm, S. T. Stewart, C. A. Simmons, and K. Aune. 1987. Interpopulation applicability of equations to predict live weight in black bears. International Conference on Bear Research and Management 7:359–362.

Zeigenfuss, L. C. 2001. Ecology of black bears in Rocky Mountain National Park: an analysis of population dynamics, diet, and habitat selection (1985–1991). Unpublished report, U.S. National Park Service, Rocky Mountain National Park, Colorado, US

Chapter 3:

Estimating population size and density of black bears in Rocky Mountain National Park, Colorado

Roger A. Baldwin, Department of Animal and Range Sciences, New Mexico State University, P.O. Box 30003 MSC 4901, Las Cruces, New Mexico 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, New Mexico 88003, USA

Chapter summary: Rocky Mountain National Park (RMNP) is home to a low density black bear (*Ursus americanus*) population that exists at > 2,400 m with a very limited growing season. A previous study (1984–1991) found black bear densities among the lowest reported (1.37–1.52 bears/100 km^2). Because of concerns of viability of this small population, we assessed population size and density of black bears from 2003–2006 to determine the current status of RMNP's black bear population. Three approaches were used to estimate population size and density: 1) minimum number known, 2) occupancy modeling, and 3) catch per unit effort (CPUE). We used information from capture and remote-sensored cameras, as well as visitor information, to derive a minimum known population estimate of 20–24 individuals. We used the median value of 22 combined with a 3,203-m area of effect around the boundary of RMNP to produce a density estimate of 1.35 bears/100 km^2. The best approximating occupancy model indicated black bear occupancy of 41.2% of RMNP. We combined the occupancy estimate with mean home-range size and overlap for male and female black bears in RMNP to determine a density estimate of 1.29 bears/100 km^2 (90% CI = 0.16–2.41). We also related CPUE to density estimates for 8 low-density populations using simple linear regression to estimate population size for black bears in RMNP. Although beyond the range of the derived model, density estimates (1.03 bears/100 km^2, 90% CI = 0.27–3.67) were well within the 90% CI for occupancy estimates and suggest this approach may be useful for future population monitoring. The current status of RMNP's black bear population appears to be stable, and occupancy and CPUE methods provide viable alternatives to monitor future trends in population size and distribution of black bears in RMNP.

Estimates of population size for black bears (*Ursus americanus*) are important in assessing trends and understanding dynamics of populations (Miller et al. 1997). Size and trend of the black bear population in Rocky Mountain National Park (RMNP), Colorado, is unknown although historical data indicated one of the lowest density populations recorded (1.37–1.52 bears/100 km^2; Zeigenfuss 2001). Monitoring such low-density populations is imperative, although extremely difficult (Romain-Bondi et al. 2004).

Population estimates of black bears are difficult to attain due to their low population densities, secretive nature, and use of relatively inaccessible habitat (McCutchen 1990, Costello et al. 2001, Pelton 2003, Romain-Bondi et al. 2004). Many techniques have been used to determine black bear densities, with mark-recapture techniques most frequently used (e.g., Lindzey and Meslow 1977, Young and Ruff 1982, Miller et al. 1987, Clark and Smith 1994). However, results from mark-recapture are often biased because they do not meet ≥ 1 of the assumptions or do not clearly delineate the area used by the population (Miller et al. 1997, Pelton 2003). In particular, mark-recapture methods do not work well for low-density populations, as it is difficult to establish enough capture-recapture events to provide valid estimates (Seber 1982, Romain-Bondi et al. 2004).

Enumerating the minimum number known may be a more appropriate method and could provide realistic estimates of population size (Beck 1991, McCutchen 1993). Enumerating bears can be accomplished from a variety of methods including capture (Beck 1991, Costello et al. 2001) and camera trapping (Beck 1997, Martorello et al. 2001). Additionally, physical descriptions of black bears are often provided by visitors to National Parks and can provide evidence of unidentified black bears in low-density populations. Utilizing several methods to identify black bears should provide a more robust approach for assessing population size (e.g., Grogan and Lindzey 1999, Noyce et al. 2001). Additionally, capture-related enumeration also allows determination of the effort needed to capture individuals, and catch per unit effort (CPUE) has been used to relate grizzly bear (*Ursus arctos*) detection to density estimates using regression techniques (Romain-Bondi et al. 2004). This approach proved to be effective at estimating density and population size for extremely low-density populations and may be applicable to RMNP.

An alternative approach would be to estimate the proportion of an area occupied by black bears through the use of presence-absence data. Various methods have been used to assess presence-absence of bears, including the use of remote-sensored cameras (Beck 1997, Martorello et al. 2001); these methods have become more prevalent in the last 10–15 years (Wintle et al. 2005). However, failure to detect individuals at sampling locations will underestimate occupancy (MacKenzie et al. 2002, Gu and Swihart 2004). Recently, a new approach has been developed that incorporates imperfect detection into occupancy estimates, thus resulting in a less-biased model (MacKenzie et al. 2005). This approach also allows the user to incorporate habitat variables in the form of covariates into occupancy analyses, thus improving occupancy estimates. Once derived, occupancy values can be related to home-range size and overlap to estimate number of individuals (Augeri et al. 2006). Such estimates can be more robust than those derived from other approaches.

Maintaining viable populations of all wildlife species is fundamental to National Park management (National Park Service 1988). Black bears are a valuable resource in RMNP because of high existence, recreational, and aesthetic values. However, current population sizes are unknown but low, limiting effective management polices for black bears in RMNP. Because of the difficulty in estimating and monitoring large carnivores at very low population densities, using multiple estimators is desirable due to the potential for corroboration of estimates. I therefore assessed population size and density of black bears in RMNP from 2003–2006 using 3 estimators: 1) minimum number known, 2) occupancy modeling, and 3) CPUE. I related these values to previous estimates to determine the apparent stability of RMNP's black bear population. Corroboration of values from the differing approaches should provide conservative estimates for black bear management in RMNP and should provide the framework for future monitoring strategies.

METHODS

Capture efforts

I used modified Aldrich foot snares to capture black bears, with a culvert trap and wire box trap also used opportunistically in heavier human-use areas. I baited snares and traps with sardines and a sweet attractant (usually honey or molasses) and checked snares daily. Primary capture efforts occurred from late June–early October 2003 and early June–mid August 2004–2006. Additional efforts occurred opportunistically from mid August to late October 2004–2006. I anesthetized bears with a 5:1 mixture of ketamine hydrochloride and xylazine hydrochloride (200 mg ketamine and 40 mg xylazine per ml). Once sedated, I sexed, weighed, fitted bears with a VHF radio collar (Advanced Telemetry Systems, Isanti, Minnesota, USA) containing a mortality sensor, and ear tagged individuals for visual identification.

Camera operation

I used ArcView 3.3 (Environmental Systems Research Institute, Inc., Redlands, California, USA) to design a saturation trapping grid for camera sites throughout the study area. I placed cameras in grids with camera locations spaced approximately 5 km apart, which equated to the diameter of the approximate minimum black bear home-range size in RMNP (Zeigenfuss 2001), to ensure that no potential home-range of a black bear was excluded from the camera-trapping grid (Karanth and Nichols 1998). When a pre-selected site was inappropriate (i.e., located on tundra, rocky cliff, etc.), I selected the closest appropriate site to place the camera.

I used 25 passive infrared-triggered cameras (DeerCam®, Non Typical, Inc., Park Falls, Wisconsin, USA) loaded with 24 exposure 400 ASA film and programmed cameras to record date and time on photographs. I set time delays on cameras at 2–5 min intervals to maximize repeat photographs while reducing the chance that a single roll of film would be used before it could be replaced. I attached baits consisting of burlap sacks containing sardines and a sweet attractant (usually honey or molasses) to a tree approximately 2 m above the ground and 3–5 m from the camera. I checked film, bait, and batteries weekly and removed the camera-sets after 2 weeks for a total of 14 days of operation per site. Occasionally, I left cameras operational for longer durations due to logistical constraints but cameras were operational for a minimum of 14 days in all but 2 cases (10 days for 1 location in 2004; 13 days for 1 location in 2005). Camera trapping dates were from 10 August–25 October 2004; 12 August–27 October 2005; and 8 August–20 October 2006 with 57 sites sampled each year.

Population and density estimation

I determined a minimum number known estimate (Elowe 1987) based on captured black bears and unique individuals identified from remote-sensored cameras. Cubs of the year were excluded from this estimate. Although non-captured individuals were unmarked, I was confident that I could individually identify most bears based on size and highly variable color patterns given the low number of individuals in the population. Nonetheless, I could not conclusively differentiate some bears in some photographs. To be conservative, I considered the indistinguishable bears as the same individual. In addition, I used physical descriptions of bears from RMNP visitor reports to determine the presence of additional unidentified bears. These additional bears were added to the minimum number known to provide minimum estimate of population size. I constructed a 3,203-m buffer (radius of mean female 95% minimum convex polygon [MCP] home-range size for RMNP; see Chapter 1) around the boundary of RMNP in ArcView 3.3 (Environmental Systems Research Institute, Inc., Redlands, California, USA) to serve as the area of effect and added this to the total area of RMNP for density estimation. Finally, I divided estimated population size by the total area (1,627 km^2) to derive a density estimate.

I also used an occupancy modeling approach to corroborate population and density estimates. This approach incorporates imperfect detection of bears at camera sites and results in an unbiased occupancy model (MacKenzie et al. 2005). Occupancy modeling allows the user to incorporate habitat variables in the form of covariates to strengthen occupancy estimates (MacKenzie et al. 2002). For habitat attributes, I used covertypes (Table 1) developed from GIS coverages of RMNP and surrounding areas provided by RMNP staff (R. Thomas, RMNP; unpublished data) and created a 400-m buffer around all human-use areas (trails, roads, campsites, and other developed areas) to assess their impact on black bear occurrence at the landscape scale. I also selected 7 landscape metrics (Table 2) based on their depiction of important landscape factors for bears (Linke et al. 2005) to relate to bear occupancy. I calculated all landscape variables using the Patch Analyst extension (Elkie et al. 1999) in ArcView 3.3 (Environmental Systems Research Institute, Redlands, California, USA).

I related black bear occurrence to covertypes and landscape metrics at the home-range scale through the use of a 32.2 km^2 sampling window around the camera location and used data collected within this buffer in subsequent analyses. I selected this window size to represent the average home-range size of female black bears in RMNP (see Chapter 1). All covertypes represented the proportion of the window covered by their respective class. Last, I included a year effect in analyses to determine if occurrence varied by year, and camera sites were separated

Table 3.1. Description of covertypes used to estimate bear occupancy for Rocky Mountain National Park, Colorado.

Covertype	Description
Herbaceous upland	Dry, open meadows
Herbaceous wetland	Herbaceous communities found on wetland or marshy sites
Mesic shrublands	Shrublands lining streambanks and valley bottoms
Xeric shrublands	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/fir species along riparian or seasonally flooded areas
Mixed conifer	Characterized by codominance of two or more 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 can be codominant
Rock	Characterized by rock, bare soil, or snow
Non-vegetated surface	Included areas covered by roads, trails, and campsites

Table 3.2. List of landscape metrics and associated descriptions related to black bear occurrence in Rocky Mountain National Park, Colorado.

Variable	Description
Patch density	Number of patches/km^2
Edge density	Meters of edge/ha
Total core area index	Measure of the amount of core area on the landscape
Area-weighted mean shape index	Measure of shape complexity
Shannon’s diversity index	Measure of relative patch diversity
Shannon’s evenness index	Measure of patch distribution and abundance
Interspersion juxtaposition index	Measure of patch adjacency

into western and eastern subdivisions of RMNP to assess large-scale differences in precipitation and associated vegetative communities caused by orographic lift of air masses.

For occupancy analyses, I used model 1 (assumes Markovian changes in occupancy) in program PRESENCE (MacKenzie et al. 2003). I used Spearman rank correlations to assess collinearity among variables; if variables were correlated at $r_s \geq 0.70$, only the variable with the lower AIC value was included in further analyses to reduce redundancy (Agresti 1996). Wald χ^2 statistics were computed for variables in models; only models with all variables significant at $\alpha < 0.10$ were considered competing models. I compared resultant models using Akaike's Information Criterion differences (ΔAIC) to determine habitat factors most strongly related to occurrence (Burnham and Anderson 1998). Following information criterion protocol, only models with ΔAIC's < 4 were considered competing models, with maximum rescaled generalized R^2 values (Nagelkerke 1991) computed to aid us in model selection. I used odds ratios to interpret relationships of habitat correlates to black bear occurrence.

Once I determined the best model, I estimated male and female black bear density by relating occupancy (divided by 2 to separate by sex) values to average home-range size and overlap for males (95% MCP home-range size = 68.0 km^2; overlap of 95% MCP home-ranges = 10.8%; see Chapter 1) and females (95% MCP home-range size = 32.2 km^2; overlap of 95% MCP home-ranges = 32.5%; see Chapter 1) through the following equation:

$$\text{minimum density} = (\Psi / 2) \times 100 \text{ km}^2 / [\text{HRS} \times (1 - \text{HRO})]$$

where Ψ = percentage of area occupied, HRS = home-range size, and HRO = percentage of home-range overlap (Augeri et al. 2006). I then combined these values to estimate total black bear density/100 km^2.

Last, I used linear regression (Zar 1999) to relate CPUE to density estimates for all known studies of black bears in the U.S. that provided information on CPUE and reported densities of < 20 bears/100 km^2 (Table 3). I defined CPUE as the number of unique black bears captured/1000 trap nights; density estimates (excluding cubs) were derived through different methods including Bowden's estimator, Lincoln-Peterson estimator, minimum number known, modified Peterson estimator, and population reconstruction (Table 3). I would have preferred utilizing studies that used the same method for estimating density, but such standardization was not possible given limited sample locations. Such variation may weaken results but should not over-inflate model fit. All models were log-transformed to represent a curvilinear relationship (Romain-Bondi et al. 2004) and residual plots were checked to assess outliers. I constructed an initial model with RMNP included to assess fit; an additional model excluding RMNP was constructed to assess the reliability of the model to predict density estimates for my study site.

RESULTS

I totaled 3,617 trap nights (2003 = 934, 2004 = 1,222, 2005 = 860, 2006 = 601) resulting in 16 total captures (2003 = 8, 2004 = 1, 2005 = 4, 2006 = 3) of 14 individual black bears (8 female, 6 male). Of these captures, 14 were in snares, and 1 each in culvert and wire box traps. Although I exerted greater trapping effort in the western portion of the park (western: 2003 = 0, 2004 = 1,019, 2005 = 619, 2006 = 392, and total = 2,030 trap nights; eastern: 2003 = 934, 2004 = 203, 2005 = 241, 2006 = 209, and total = 1,587 trap nights), the total number of captures was greater in eastern RMNP (west = 3, east = 13). This yielded 1 black bear capture per 676.7 and 132.3 trap nights for the western and eastern portions of RMNP, respectively, for a total of 1 capture per 241.1 trap nights for the entire park. The bear captured in the cage trap was excluded

Table 3.3. List of studies and locations used to relate catch per unit effort (CPUE, number of unique bears captured/1000 trap nights) to density (bears/100 km^2) of black bears.

Study	Location	CPUE	Density[a]
This study	Colorado	6.9	1.4
Grogan and Lindzey 1999	Wyoming	22.4	2.5
Orlando 2003, Brown 2004	Florida	16.9	2.9
Harter 2001	South Carolina	21.7	5.7
Costello et al. 2001	Western New Mexico	42.3	9.4
Cunningham and Ballard 2004	Arizona	43.8	12.9
Frost 1990	Utah	29.1	12.9
Costello et al. 2001	Northern New Mexico	48.2	17.0
Kasworm and Manley 1988	Montana	38.9	17.4

[a] Density estimators included: Bowden's estimator = Grogan and Lindzey 1999; Lincoln-Peterson estimator = Kasworm and Manley 1988 (excluding cubs), Harter 2001, Brown 2004; minimum number known = Frost 1990, current study; modified Peterson estimator = Cunningham and Ballard 2004; population reconstruction = Costello et al. 2001.

from CPUE values as no measurable effort was expended on my part (incidental capture by D. Hunter, United States Geological Survey, Fort Collins, Colorado, USA).

I operated cameras for 2,608 days (850, 868, and 890 days in 2004, 2005, and 2006 respectively) resulting in visual identification of a minimum of 11 additional black bears from 13 total bear visits (2004 = 5, 2005 = 5, 2006 = 3) to 7 sites in the western portion of RMNP and 11 total visits (2004 = 1, 2005 = 5, 2006 = 4) to 8 sites in the eastern portion of the park (Fig. 1). This yielded 1 visit per 89.1 and 131.8 camera nights for western and eastern RMNP, respectively, for a total of 1 visit per 108.7 camera nights.

Although, the largest number of individuals captured occurred in the eastern portion of RMNP (12 eastern, 2 western), the distribution of photographed individuals was less variable (6 eastern, 5 western). Two collared black bears were harvested with 2 other recorded mortalities of collared individuals from unknown causes resulting in a minimum number of 21 individuals (15 on the eastern side, 6 on the western side). Two of these black bears were photographed on the periphery of the park (< 1 km from boundary) and were not subsequently observed again; they may not have extensively used park property so I reduced the minimum number known value by 1 (half of 2) to account for this probability. Based on location and physical descriptions of black bears given in visitor reports, it is likely there were another 1–2 bears on both the western and eastern portions of the park resulting in a total population size of 20–24 black bears (excludes cubs). It should be noted this estimate assumed no additional mortality during the sampling period. Annual survival was relatively high during my study (adults = 0.96 [SE = 0.04], subadults = 0.83 [SE = 0.14]; see Chapter 4). Therefore, I assumed 22 individuals in the population, which resulted in a density estimate of 1.35 bears/100 km^2 in RMNP.

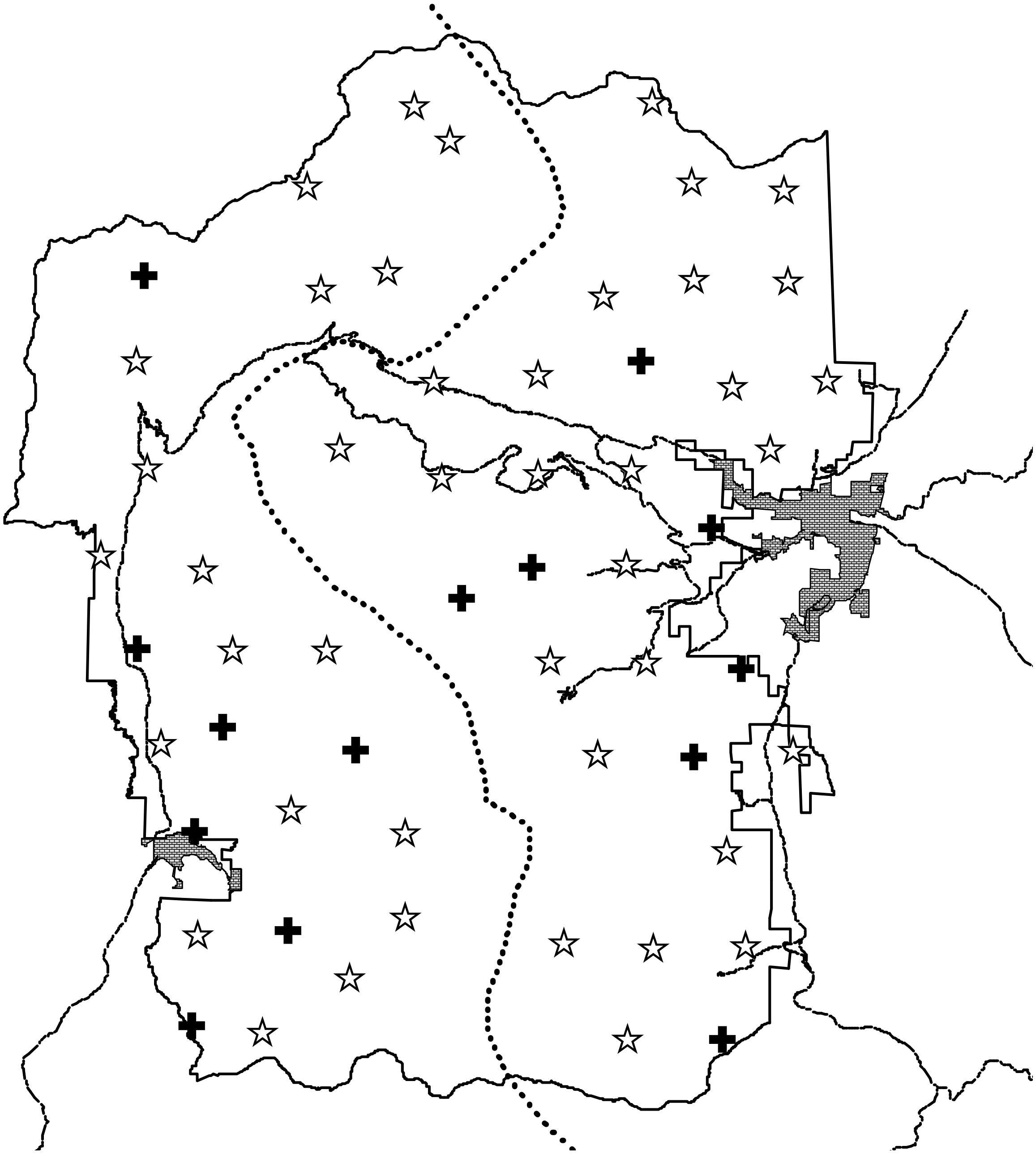

Figure 3.1. Map depicting camera locations operated from 2004–2006 to detect black bear occurrence in Rocky Mountain National Park, Colorado. Camera locations with bear visits are depicted by crosses, while those without bear visits are marked with stars. The dotted line demarcates the western and eastern subdivisions of RMNP, while the dashed lines represent park roads and highways.

The best occupancy model ($\chi^2 = 13.6$, $P < 0.001$, $R^2 = 0.10$; Table 4) included the subdivision of RMNP ($\chi^2 = 12.3$, $P < 0.001$; $\beta = -3.902$ [SE = 1.115]; odds ratio = 0.020 [90% CI = 0.003–0.130]), greater amounts of non-vegetated surfaces ($\chi^2 = 8.1$, $P = 0.004$; $\beta = 1.155$ [SE = 0.406]; odds ratio = 3.2 [90% CI = 1.6–6.3]), krummholz ($\chi^2 = 3.1$, $P = 0.080$; $\beta = 0.291$ [SE = 0.166]; odds ratio = 1.34 [90% CI = 1.01–1.77]), and limber pine stands ($\chi^2 = 9.4$, $P = 0.002$; $\beta = 0.306$ [SE = 0.100]; odds ratio = 1.4 [90% CI = 1.1–1.6]), and less area associated with mesic shrublands ($\chi^2 = 3.3$, $P = 0.070$; $\beta = -0.321$ [SE = 0.177]; odds ratio = 0.73 [90% CI = 0.54–0.98]). Alternative models (Table 4) included similar variables but were not considered further given their higher AIC scores and a reduction of ≥ 20% in R^2 values. Additionally, I saw no effect of year and no difference in occupancy between western and eastern portions of RMNP resulting in an occupancy rate of 41.2% (SE = 21.8). When combined with home-range size and overlap, I determined density estimates of 0.95 female bears/100 km^2 (90% CI = 0.12–1.77) and 0.34 male bears/100 km^2 (90% CI = 0.04–0.64) for a total of 1.29 bears/100 km^2 (90% CI = 0.16–2.41).

Given the likely presence of trap-shy bears in the western portion of the study area (illustrated by large difference for CPUE between western and eastern RMNP from trapping efforts and large disparity between trapping and camera CPUE for western RMNP), I used CPUE (6.9 bears/1000 trap nights) only from eastern localities for regression analyses. Based on residual plots, I considered the study site in Wyoming (Grogan and Lindzey 1999) an outlier and excluded it from further analyses. Resultant models indicated a strong relationship between CPUE and density ($F_{1,6} = 54.0$, $P < 0.001$; Fig. 2). The model excluding RMNP also yielded a strong relationship ($F_{1,5} = 17.5$, $P = 0.009$; Fig. 2) with predicted density values (1.03 bears/100 km^2, 90% CI = 0.27–3.67) falling within the 90% CI derived from the occupancy model.

Table 3.4. Summary of selected occupancy models relating black bear presence to habitat attributes in Rocky Mountain National Park (RMNP), Colorado. Values reported include likelihood ratio χ^2 statistics (χ^2) and associated *P*-values (*P*), Akaike's Information Criterion (AIC) values and the difference in AIC when compared to the top models (ΔAIC), and maximum rescaled generalized R^2 (R^2).

Model[a]	χ^2	*P*	AIC	ΔAIC	R^2
sub, limp, nv, ms, k	13.6	<0.001	254.1	0.0	0.10
sub, limp, nv, ms	10.3	0.001	255.4	1.3	0.08
sub, limp, nv, k	9.1	0.003	256.6	2.5	0.07
sub, limp, nv	6.5	0.010	257.2	3.1	0.05

[a] Variable notation: sub = west vs. east subdivision of RMNP, limp = limber pine, nv = non-vegetated surface, ms = mesic shrublands, k = krummholz.

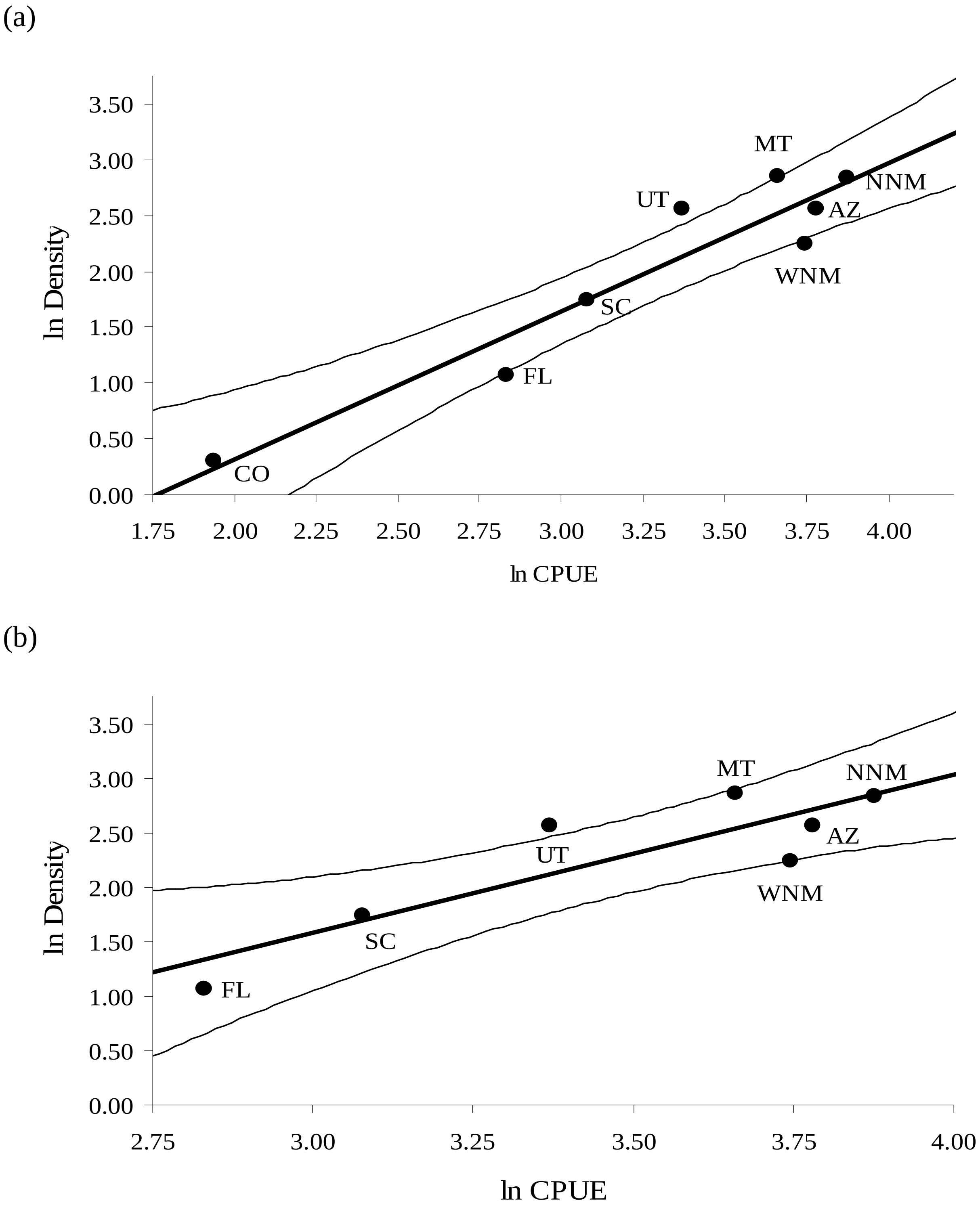

Figure 3.2. Regression and 95% CI relating ln catch per unit effort (number of black bears captured/1000 trap nights, CPUE) to ln density (number of black bears/100 km^2): (a) includes RMNP study site, (b) excludes RMNP study site. Model equations: (a) ln(Density) = 1.326 × (ln[CPUE]; SE = 0.347) – 2.337, $R^2 = 0.900$; and (b) ln(Density) = 1.451 × (ln[CPUE]; SE = 0.181) – 2.780, $R^2 = 0.777$.

Additionally, the means for each method (1.35, 1.29, and 1.03 bears/100 km^2) were similar, indicating that methods produced corroborating mean density estimates for black bears in RMNP.

DISCUSSION

Accurate population and density estimates of black bears are difficult to obtain given the need for intensive sampling effort and likely violations of assumptions of most approaches (Romain-Bondi et al. 2004). Although total enumeration of a population is often difficult, it may be the best alternative for extremely low density populations (Beck 1991, McCutchen 1993), particularly when intensive capture efforts are required for estimation of other population parameters (i.e., survival, recruitment, home-range size, etc.). My minimum number known estimates indicate RMNP had the lowest density of black bears reported in the literature (1.23–1.48 bears/100 km^2), with these estimates consistent with previous reported densities for RMNP (1.37–1.52 bears/100 km^2; Zeigenfuss 2001). Although the minimum number known estimate required significant effort, I felt it was the most accurate method given the additional knowledge I obtained about the population.

Although confidence intervals were relatively wide for density estimates, the occupancy method yielded similar results (1.29 bears 100/km^2), corroborating minimum number known estimates. Incorporating additional sampling locations would likely reduce the variability of these estimates, thus increasing confidence in this approach. Additionally, using occupancy to estimate population size and density has several advantages over total enumeration. First, percent occupancy can be used to monitor long-term trends in populations without deriving density estimates (MacKenzie and Nichols 2004, MacKenzie et al. 2005), thereby eliminating the need to estimate home-range size and overlap. Secondly, the occupancy approach utilizes non-invasive techniques that reduce stress and impact on sampled bears (Mills et al. 2000). Also, less effort and cost are required to estimate population size once home-range size and overlap have been determined. Nonetheless, home-range size and overlap should be re-evaluated periodically to account for changes in preferred habitats, human-use components, etc.

A further advantage of the occupancy approach is that habitat relationships can also be assessed through occupancy modeling (MacKenzie 2006). I observed increased occurrence associated with west-side locations with greater amounts of non-vegetated surfaces, limber pine stands, and krummholz, and less area associated with mesic shrublands. West-side localities are more mesic given orographic precipitation effects, potentially yielding more abundant vegetation and subsequent food sources. However, neither current findings nor previous work (Zeigenfuss 2001) indicated any difference in density estimates between eastern and western portions of RMNP (east = 1.37 bears/100 km^2, west = 1.52 bears/100 km^2; Zeigenfuss 2001). Additionally, my investigation indicated no difference in occupancy estimates between eastern and western RMNP, suggesting that at least the precipitation pattern had little effect on population productivity. Interestingly, the effort required to snare black bears in western RMNP was much greater than for cameras; CPUE values derived from snaring and camera trapping were almost equivalent for eastern RMNP. This suggests substantial trap-shyness for black bears in western RMNP, the reason for which is unknown but could be related to increased hunting pressure compared to eastern localities or previous experience with capture techniques.

The correlation with non-vegetated surfaces likely reflected an affinity for human-use areas (i.e., campgrounds, residences, etc.; see Chapter 7). McCutchen (1990) noted an avoidance of such areas in RMNP in the late 1980’s. My results suggest RMNP’s black bear population was more habituated to human-use areas and may actually be located more frequently in such areas (see Chapter 7). A similar situation was noted in the Sierra Nevada-Great Basin interface in Nevada, as black bear distributions shifted substantially from traditional wildlands to an urban setting over the course of 10–15 years (Beckmann and Berger 2003a, b). This shift was in response to abundant anthropogenic food sources in urban areas and provides a likely explanation for increased occurrence in non-vegetated areas given increased occurrence of anthropogenic foods in contemporary black bear diets (historic = 0.9% of bear scats, contemporary = 14.2%; Chapter 6).

The correlation with krummholz and limber pine stands may reflect the relationship between dates sampled and elevation. In mountainous terrain, black bears frequently move higher in elevation ($\bar{x}$ elevation: krummholz = 3,461 m, SE = 1.5; limber pine = 3,125, SE = 8.6; other forested covertypes = 2,980, SE = 3.2) as seasons progress into summer and early autumn. These movement patterns typically mirror the ripening of soft mast (e.g., raspberry [*Rubus* spp.], chokecherry [*Prunus virginiana*]) and other food sources (Beck 1991). Additionally, limber pine nuts may be an important food for black bears in RMNP when other food sources are limited (McCutchen 1996), although use of limber pine stands was generally negatively related to black bear condition in RMNP (see Chapter 7). The avoidance of mesic shrublands may also be related to season. Such areas contain few food sources from late summer through autumn but may be more important during spring when herbaceous growth is higher in protein and more easily digested (Eagle and Pelton 1983, Rogers et al. 1988).

Relationships between CPUE and density estimates further corroborated minimum number known densities (1.03 versus 1.35 bears/100 km^2, respectively) and provided another alternative for monitoring low-density populations. I observed relatively strong relationships between CPUE and density estimates using curvilinear models. A similar relationship was observed for grizzly bears ($R^2 = 0.927$) in the North Cascade Ecosystem of Washington and British Columbia using DNA hair-sampling techniques (Romain-Bondi et al. 2004), where a non-linear model fit data better given the curvilinear relationship between home-range size and density. This relationship was also likely for black bears given the known influence of density on home-range size (Oli et al. 2002, Pelton 2003). Additionally, model fit from the Romain-Bondi et al. (2004) study was only slightly better than what I observed. This was unexpected given the nature of the sampling protocols. Hair-snaring efforts tend to be more systematic, whereas capture efforts are often focused in areas where CPUE is expected to be greatest. Also, the chance of false or missed detections may be greater for capture efforts (i.e., missed captures or trap-shy individuals) than for hair-snaring and other remote-sampling techniques. Further, density estimates were derived from a wide range of methods in the studies I analyzed, whereas those from Romain-Bondi et al. (2004) were all calculated using either radio telemetry or program CAPTURE's best-fit population estimation models. These differences in sampling protocol should decrease the predictive power of my models (Seber 1982), yet they remained high suggesting a robust relationship between density and CPUE among low density black bear populations.

A major purpose for relating CPUE to density was to establish a method for estimating density when densities are too low to be estimated by other means. Because 1 grizzly bear population was too small to be determined by conventional means, Romain-Bondi et al. (2004) estimated density for this population outside the range of their estimated data given that they had little reason to assume such relationships did not hold true beyond the sampled range. Although extrapolation beyond the range of estimated data should be viewed with caution, models excluding data from my study predicted density estimates well within the 90% CI of values derived for RMNP from the occupancy approach. Further, the slope of models with and without RMNP did not differ ($t = 0.39$, $P = 0.704$), thus providing additional evidence for the validity of this approach. Nonetheless, unless populations are too small to be estimated by other techniques, I do not recommend using CPUE models as the only approach for monitoring populations, but rather to corroborate estimates derived from other approaches (i.e., occupancy, Jennelle et al. 2002).

MANAGEMENT IMPLICATIONS

Corroborated density (1.03–1.35 bears/100 km^2) of black bears in RMNP was the lowest recorded for any known population, but apparently changed little in the last 15–20 years, indicating a relatively stable population. However, contemporary reproductive data suggests the potential for substantial growth in population size over the next 10 years (2016 median population size = 63; see Chapter 4). Although RMNP's black bear population is unlikely to attain such a high population level during this time frame, continued monitoring is needed to assess changes in distribution and population size. Of principal importance is monitoring the association of black bears with human-use areas (see Chapter 7). Continued shifts into such areas could result in higher mortality rates from hunting (Samson and Huot 1998), vehicular collisions (Beckmann and Berger 2003b, Freedman et al. 2003), and removal of problem bears (McCarthy and Seavoy 1994), and could potentially result in the decline of RMNP's black bear population due to emigration out of wildland areas (Beckmann and Berger 2003a, b). If bears continue to shift core-areas into human-use sites, the implementation of mitigation efforts (i.e., increasing early successional habitats; see Chapter 7) may be required to reduce bear-human conflicts. Continued use and periodic reassessment of occupancy and CPUE models can allow RMNP staff to effectively monitor the local black bear population to assess trends in population size and distribution of black bears in RMNP.

LITERATURE CITED

Agresti, A. 1996. An introduction to categorical data analysis. John Wiley & Sons, New York, New York, USA.

Augeri, D. M., M. Fisher, D. J. Chivers, and J. A. Royle. 2006. Good estimates of density: a response to Garshelis and McLellan. International Bear News 15:8–11.

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

Beck, T. D. I. 1997. Development of black bear inventory techniques. Colorado Division of Wildlife Federal Aid Progress Report W-153-R-10, WP5A, J2. Fort Collins, Colorado, USA.

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

Brown, J. H. 2004. Challenges in estimating size and conservation of black bear in west-central Florida. Thesis, University of Kentucky, Lexington, Kentucky, USA.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York, USA.

Clark, J. D., and K. G. Smith. 1994. A demographic comparison of two black bear populations in the interior highlands of Arkansas. Wildlife Society Bulletin 22:593–603.

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, New Mexico, USA.

Cunningham, S. C., and W. B. Ballard. 2004. Effects of wildfire on black bear demographics in central Arizona. Wildlife Society Bulletin 32:928–937.

Eagle, T. C., and M. R. Pelton. 1983. Seasonal nutrition of black bears in the Great Smoky Mountains National Park. International Conference on Bear Research and Management 5:94–101.

Elkie, P. C., R. S. Rempel, and A. P. Carr. 1999. Patch Analyst User's Manual. Technical Manual TM-002, Northwest Science and Technology, Ontario Ministry of Natural Resources, Thunder Bay, Canada.

Elowe, K. D. 1987. Factors affecting black bear reproductive success and cub survival in Massachusetts. Dissertation, University of Massachusetts, Amherst, Massachusetts, USA.

Freedman, A. H., K. M. Portier, and M. E. Sunquist. 2003. Life history analysis for black bears (*Ursus americanus*) in a changing demographic landscape. Ecological Modelling 167:47–64.

Frost, H. C. 1990. Population and reproductive characteristics of black bears on an isolated mountain in southeastern Utah. Thesis, Brigham Young University, Provo, Utah, USA.

Grogan, R. G., and F. G. Lindzey. 1999. Estimating population size of a low-density black bear population using capture-resight. Ursus 11:117–122.

Gu, W., and R. K. Swihart. 2004. Absent or undetected? Effects of non-detection of species occurrence on wildlife-habitat models. Biological Conservation 116:195–203.

Harter, W. H., III. 2001. Biology of the black bear in the northern coastal plain of South Carolina. Thesis, Clemson University, Clemson, South Carolina, USA.

Jennelle, C. S., M. C. Runge, and D. I. MacKenzie. 2002. The use of photographic rates to estimate densities of tigers and other cryptic mammals: a comment on misleading conclusions. Animal Conservation 5:119–120.

Karanth, K. U., and J. D. Nichols. 1998. Estimation of tiger densities in India using photographic captures and recaptures. Ecology 79:2852–2862.

Kasworm, W. F., and T. Manley. 1988. Grizzly bear and black bear ecology in the Cabinet Mountains of Northwest Montana. Montana Department of Fish, Wildlife, and Parks, Helena, Montana, USA.

Lindzey, F. G., and E. C. Meslow. 1977. Population characteristics of black bears on an island in Washington. Journal of Wildlife Management 41:408–412.

Linke, J., S. E. Franklin, F. Huettmann, and G. B. Stenhouse. 2005. Seismic cutlines, changing landscape metrics and grizzly bear landscape use in Alberta. Landscape Ecology 20:811–826.

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

MacKenzie, D. I., and J. D. Nichols. 2004. Occupancy as a surrogate for abundance estimation. Animal Biodiversity and Conservation 27:461–467.

MacKenzie, D. I., J. D. Nichols, J. E. Hines, M. G. Knutson, and A. B. Franklin. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. Ecology 84:2200–2207.

MacKenzie, D. K., 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.

MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2005. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Academic Press, San Diego, California, USA.

Martorello, D. A., T. H. Eason, and M. R. Pelton. 2001. A sighting technique using cameras to estimate population size of black bears. Wildlife Society Bulletin 29:560–567.

McCarthy, T. M., and R. J. Seavoy. 1994. Reducing nonsport losses attributable to food conditioning: human and bear behavior modification in an urban environment. International Conference on Bear Research and Management 9:75–84.

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.

McCutchen, H. E. 1993. Ecology of high mountain black bear population in relation to land use at Rocky Mountain NP. Park Science 13:25–27.

McCutchen, H. E. 1996. Limber pine and bears. Great Basin Naturalist 56:90–92.

Miller, S. D., E. F. Becker, and W. B. Ballard. 1987. Black and brown bear density estimates using modified capture-recapture techniques in Alaska. International Conference on Bear Research and Management 7:23–35.

Miller, S. D., G. C. White, R. A. Sellers, H. V. Reynolds, J. W. Schoen, K. Titus, V. G. Barnes, Jr., T. B. Smith, R. R. Nelson, W. B. Ballard, and C. C. Schwartz. 1997. Brown and black bear density estimation in Alaska using radiotelemetry and replicated mark-resight techniques. Wildlife Monographs 133.

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

Nagelkerke, N. J. D. 1991. A note on a general definition of the coefficient of determination. Biometrika 78:691–692.

National Park Service. 1988. Management policies. U. S. Department of the Interior, Washington D. C., USA.

Noyce, K. V., D. L. Garshelis, and P. L. Coy. 2001. Differential vulnerability of black bears to trap and camera sampling and resulting biases in mark-recapture estimates. Ursus 12:211–226.

Oli, M. K., H. A. Jacobson, and B. D. Leopold. 2002. Pattern of space use by female black bears in the White River National Wildlife Refuge, Arkansas, USA. Journal for Nature Conservation 10:87–93.

Orlando, M. A. 2003. The ecology and behavior of an isolated black bear population in west central Florida. Thesis, University of Kentucky, Lexington, Kentucky, USA.

Pelton, M. R. 2003. Black bear (*Ursus americanus*). Pages 547–555 *in* G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, editors. Wild mammals of North America: biology, management, and conservation. Second edition, revised. Johns Hopkins University Press, Baltimore, Maryland, USA.

Rogers, L. L., G. A. Wilker, and A. W. Allen. 1988. Managing northern forests for black bears. Pages 36–42 *in* T. W. Hoekstra and J. Capp, editors. Integrating forest management for wildlife and fish. U.S. Department of Agriculture, Forest Service, General Technical Report NC-122.

Romain-Bondi, K. A., R. B. Wielgus, L. Waits, W. F. Kasworm, M. Austin, and W. Wakkinen. 2004. Density and population size estimates for North Cascade grizzly bears using DNA hair-sampling techniques. Biological Conservation 117:417–428.

Samson, C., and J. Huot. 1998. Movements of female black bears in relation to landscape vegetation type in southern Québec. Journal of Wildlife Management 62:718–727.

Seber, G. A. F. 1982. The estimation of animal abundance. Second edition. Charles Griffin and Company, London, United Kingdom.

Wintle, B. A., R. P. Kavanagh, M. A. McCarthy, and M. A. Burgman. 2005. Estimating and dealing with detectability in occupancy surveys for forest owls and arboreal marsupials. Journal of Wildlife Management 69:905–917.

Young, B. F., and R. L. Ruff. 1982. Population dynamics and movements of black bears in east central Alberta. Journal of Wildlife Management 46:854–860.

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

Zeigenfuss, L. C. 2001. Ecology of black bears in Rocky Mountain National Park: an analysis of population dynamics, diet, and habitat selection (1985–1991). Unpublished report, U.S. National Park Service, Rocky Mountain National Park, Colorado, USA.

Chapter 4:

Survival, reproduction, and trends of black bears in Rocky Mountain National Park, Colorado

Roger A. Baldwin, Department of Animal and Range Sciences, New Mexico State University, P.O. Box 30003 MSC 4901, Las Cruces, New Mexico 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, New Mexico 88003, USA

Chapter summary: Historically, Rocky Mountain National Park (RMNP) has supported a small black bear (*Ursus americanus*) population of low population productivity. Increased development around the periphery and visitor use of RMNP could alter survival and productivity demographics of this population. We investigated contemporary survival and productivity parameters for RMNP's black bear population from 2003–2006 and compared these values to historic levels (1984–1991) and population means throughout the western U.S. Results indicated the contemporary black bear population exhibited earlier age of first reproduction (historical = 7.5 years, contemporary = 5.5 years) and higher cub survival (historical = 0.43, contemporary = 0.71); litter size and adult and subadult survival were similar between periods. This resulted in higher recruitment (yearlings/female/year; historical = 0.34, contemporary = 0.56), a greater number of reproductive years (historical = 7.5, contemporary = 9.5), and higher reproductive output per female lifetime (number of cubs reaching reproductive age/female reproductive lifetime; historical = 0.73 [90% CI = 0.26–1.72], contemporary = 1.80 [90% CI = 0.75–3.49]). These contemporary values were similar to other western U.S. populations. Additionally, stochastic population modeling predicted a much higher probability of an increasing population for the contemporary period (90% probability of growth from 22 to ≤ 53 versus 19 for a 10 year simulation). This increased productivity may be related to better nutritional condition of reproductive females during the contemporary period (weight: historical = 60 kg, contemporary = 68 kg; body fat: historical = 15%, contemporary = 23%), likely due to greater use of anthropogenic food sources. Black bears in RMNP have much greater growth potential than observed historically, due primarily to increased productivity likely attributable to enhanced nutrition.

Black bears (*Ursus americanus*) are rare in Rocky Mountain National Park (RMNP), but reasons for low population size are unknown. Population growth is determined by the interaction of survival rates and productivity, but survival and reproductive rates can be difficult to collect for cryptic, long-lived species (Sorensen and Powell 1998) with low reproductive capability (Noyce and Garshelis 1994) such as black bears. However, knowledge of these parameters is necessary to determine whether populations are limited by low adult survival or low productivity.

Common causes of mortality for subadult and adult black bears include intra- and inter-specific predation (Kemp 1976, LeCount 1987, Mattson et al. 1992, Costello et al. 2001, Gunther et al. 2002), starvation (Costello et al. 2001, Pelton 2000), and old age (Pelton 2003), although legal and illegal harvest typically account for the largest proportion of adult black bear mortality (Bunnell and Tait 1985, Beck 1991, Schwartz and Franzmann 1991, 1992, Powell et al. 1996, Beringer et al. 1998, Pelton 2003). Cub mortality is influenced by habitat quality (Beecham 1980, Rogers 1987), spring nutrition (Schwartz and Franzmann 1991, Costello et al. 2003), experience of the mother (Elowe and Dodge 1989, Beck 1991), spring weather (Alt 1984, Beck 1991, Oli et al. 1997), predator numbers (including conspecifics; LeCount 1987, Rogers 1987, Beck 1991) and mast abundance in autumn (Eiler et al. 1989, Elowe and Dodge 1989, Beck 1991, Costello et al. 2003), most of which directly relate to size and nutritional condition of females and hence maternal investment (Noyce and Garshelis 1994). Yearling survival is also heavily influenced by maternal condition during their first year (McCutchen 1993, Noyce and Garshelis 1994). Therefore, adult condition has a significant effect on cub and yearling survival, although its role in adult survival is less clear.

Similarly, most reproductive parameters of black bears (i.e., age of primiparity, litter size, interbirth interval) are primarily influenced by maternal size and condition (Rogers 1987, Eiler et al. 1989, Elowe and Dodge 1989, Kolenosky 1990, Samson and Huot 1995, Beckmann and Berger 2003b, Costello et al. 2003), although the effect varies with the absolute condition of bears (Noyce and Garshelis 1994). Litter size is greatest at highest levels of condition, but rapidly declines to a stable level of 1–2 cubs/litter (Noyce and Garshelis 1994). Mean age of primiparity is lower for females in good condition, and thus can have a strong influence on overall productivity of both the individual and the population as mean condition increases (Rogers 1987, Noyce and Garshelis 1994). Maternal condition may have less effect on interbirth interval, though intervals will increase when condition drops below some low threshold level (Noyce and Garshelis 1994). Therefore, knowledge of condition indices should aid in interpretation of most, if not all population demographics, and assist in modeling population growth and trends.

Black bear populations in RMNP have remained at very low levels (< 30) for decades (T. Terrell, RMNP, personal communication). Data from the 1980's and early 1990's suggested that low population size was due to poor productivity (McCutchen 1993). Since then, trends in the black bear population are unknown, although it has likely not increased significantly. Further, continued development around RMNP and increasing visitor use of RMNP may further isolate this black bear population (Zeigenfuss 2001), which already is challenged by extremely high elevation habitats with a short growing season (McCutchen 1993). Because productivity, survival, and trends of black bears in RMNP are unknown, it is uncertain whether the bear population is viable or whether it must be maintained by immigration from outside sources to persist, which could potentially be threatened by increasing isolation of RMNP. To assess the ability of the black bear population of RMNP to persist, I determined survival and reproductive parameters of black bears in RMNP and used them to model population trends. My objectives included: 1) estimate survival for adult and subadult male and female black bears for both the historic and contemporary periods, 2) estimate reproductive parameters for the historic (1984–1991) and contemporary (2003–2006) periods, 3) relate body condition to reproductive parameters to assess their influence on these demographics, and 4) model population growth for historic and contemporary populations.

METHODS

Capture and radiotracking

I used modified Aldrich foot snares and culvert traps to capture black bears from 1984–1991 and 2003–2006. I immobilized bears with a 5:1 mixture of ketamine hydrochloride and xylazine hydrochloride (200 mg ketamine and 40 mg xylazine per ml) and fit bears with radiocollars. I placed bears into appropriate sex and age categories (subadult vs. adult); adult females were differentiated from subadults based on known age, nipple size, and nipple coloration (Beck 1991, Brooks and McRoberts 1997), while adult males were identified by larger size, obvious staining of teeth, and descended testicles (Beck 1991, Garshelis and Hellgren 1994). In years after capture, I radiotracked individuals from May through the time of den entrance. I obtained locations of bears as often as possible, with locations typically recorded a minimum of once per week. However, due to logistical constraints and movements off RMNP property, the time interval between locations was occasionally longer.

Survival and cause-specific mortality

I determined annual survival of black bears by sex and age class from radiotracking and calculated survival rates using the staggered-entry Kaplan-Meier estimator (Pollock et al. 1989). I determined causes-of-death following Bender et al. (2004) and calculated cause-specific mortality rates using the method of Heisey and Fuller (1985). Here, I attributed each death to the mid-point of each month and treated each month as a uniform 30 d time period. This allowed the overall survival estimates from both methods to be identical (Bender et al. 2004).

Cub production

I determined production and survival of cubs from late-winter den checks and from observations of cubs-at-heel. I recorded age of primiparity from known-age bears, litter interval, litter size, cub survival (number of cubs surviving to 1 year of age/total number of cubs born), natality (number of cubs/female/year), and recruitment (number of yearlings/female/year) for all females from observations and den checks of all radiocollared bears. In addition, I estimated the number of years a female was reproductively active by assuming reproductive senescence of females at age 15 and subtracting mean age of primiparity from 15. I selected this age given the mean age of females = 13 years in 1992 (S. King, personal communication via L. Zeigenfuss). Because no female mortality was documented during this period (see below), I added 2 years to this age to approximate reproductive senescence/female mortality. This value may have been an underestimate, as at least 1 female was believed alive and reproducing at 18 years of age (RMNP, unpublished data).

I estimated lifetime reproductive success by multiplying recruitment by the number of years a female was reproductively active to estimate the number of cubs a female could produce that would reach 1 year of age during her reproductive lifetime. I assumed a juvenile sex ratio of 1:1, and divided the number of cubs recruited per female lifetime by 2 to estimate the number of female cubs surviving to 1 year of age per female reproductive lifetime. I then multiplied this value by female survivorship from 1 year of age to reproductive maturity to provide an index of population viability; a value of 1.0 was needed for the female to replace herself in the population within her expected reproductive lifetime. I calculated 90% CI's around this estimate by parametric bootstrapping using the means and SE's of each independent variable (Bender et al.

1996). I compared this index between historic and contemporary periods in RMNP, and to other populations throughout the western U.S. to provide an index of population viability in RMNP.

Population modeling

I used the stochastic population modeling software POP-III (version 1.0, Fossil Creek Software, Fort Collins, Colorado, USA) to model potential population growth for both the 1985–1992 and 2003–2006 periods. Data inputs included period specific recruitment rates; subadult, adult male, and adult female survival rates; and initial size of these population segments. POP-III randomizes important parameters based on a statistic of central tendency and dispersion associated with each input. I used a uniform distribution for initial population sizes and a normal distribution for recruitment and survival rates from data collected in RMNP (see Results). To calculate initial population size I multiplied the proportion of individuals of each sex and age class (determined from captured individuals) by the estimated population size. Population size was estimated between 20–25 and 20–24 black bears for historic (Zeigenfuss 2001) and contemporary (see Chapter 3) periods, respectively. Therefore, I used the median value of 22 to standardize initial population size for both periods. I then ran 1,000 randomized simulations, and defined the probability associated with any given level of population size after the 10 year simulations. I also determined the median population size after the 10 year simulations.

RESULTS

Survival and cause-specific mortality

I had fate information from 24 radio-collared black bears (adult male = 6, adult female = 5, subadult male = 6, subadult female = 7) from 1985–1990 and 14 collared black bears (adult male = 4, adult female = 4, subadult male = 2, subadult female = 4) from 2003–2006 for survival analyses. Survival estimates between historic and contemporary periods did not differ for any cohort ($Z \leq 1.2$, $P \geq 0.20$) (Table 1). The leading cause of mortality was harvest. The harvest-specific mortality rate was 0.333 in 1985, 0.111 in 1987, 0.167 in 2004, 0.125 in 2005, and 0.000 in all other years for a mean of 0.074 over all years (1985–1990 = 0.074, 2003–2006 = 0.073). All other causes of mortality were unknown.

Cub production

Historic period.—I observed 9 litters totaling 16 cubs (8 male, 8 female; $\bar{x}$ = 1.78 cubs/litter, SE = 0.15). Interbirth intervals were not available for this time-frame though they were assumed to be close to 2 years (McCutchen 1993). I documented age of primiparity for 2 females ($\bar{x}$ = 7.5 years, SE = 0.5). Cub survival was 0.43 per McCutchen (1993); *n* and SE were not provided. Because of the absence of interbirth interval data historically, I used the value derived from the contemporary period (see below) to estimate natality at 0.79 (SE = 0.09) cubs/female/year; recruitment averaged 0.34 (SE = 0.08) yearlings/female/year.

Contemporary period.—I observed 7 cubs through 4 birthing events by collared black bears ($\bar{x}$ = 1.75 cubs/litter, SE = 0.25); 4 cubs were counted in the den while 3 were observed at heel. Of the 4 observed in dens, 2 were male and 2 were female. The sex of the other cubs was unknown. Interbirth interval for 2 females was 2.5 years (SE = 0.5). Two additional females likely reproduced in spring 2007 (body fat = 39 and 45% for each bear, respectively). Although actual reproductive status was not verified given the end of field activities, I assumed reproduction occurred given known strong relationships between body condition and reproduction (Rogers 1987, Samson and Huot 1995, Harlow et al. 2002); including these 2 females resulted in a mean interbirth interval of 2.25 (SE = 0.25) years. Age of primiparity was recorded for 1 bear (4 years). One additional female had not reproduced by age 5 when the study

Table 4.1. Survival estimates for historic (1985–1990) and contemporary (Contemp; 2003–2006) black bear populations in Rocky Mountain National Park, Colorado. Survival estimates were not different between periods for any cohort ($Z \leq 1.2$, $P \geq 0.20$).

		Adult males	Adult females	Adults combined	Subadult males	Subadult females	Subadults combined	All combined
Historic	$\bar{x}$	1.000	1.000	1.000	0.500	0.917	0.745	0.870
	SE	0.000	0.000	0.000	0.071	0.072	0.205	0.113
Contemp	$\bar{x}$	0.917	1.000	0.958	0.500	0.917	0.834	0.891
	SE	0.068	0.000	0.038	0.000	0.068	0.136	0.097

ended and was not likely to reproduce at age 6 in winter 2007 (body fat = 22%). Therefore, I estimated primiparity at 7 years for this female but acknowledge this was not measured directly, resulting in a mean age of primiparity of 5.5 (SE = 1.5) years. Cub survival was 0.71 (SE = 0.12). I estimated natality at 0.78 (SE = 0.15) cubs/female/year; recruitment averaged 0.56 (SE = 0.14) yearlings/female/year.

Population modeling

Initial population structure was skewed toward a greater proportion of subadults and fewer adults in the initial population structure from 1984–1991 (Table 2). Because estimated survival rates were 1.0 for adult females for both data collection periods, I used a survival rate of 0.95 to incorporate adult mortality in models based on levels reported for other populations (0.95–0.99, Eberhardt 2002; 0.96, Beck 1991). I also used adult male survival rates from 2003–2006 for both periods to incorporate mortality into adult males for simulations of the 1986–1992 period. All other survival estimates used in models were specific to each data collection period.

Stochastic simulations for 1993–2003 resulted in a final median population estimate of 25 (SE = 5) black bears (Table 3), with a 90% probability that the final population was ≥ 19. Modeling from 2006–2016 resulted in a median population size of 63 (SE = 8) black bears (Table 3), with a 90% probability that the final population was ≥ 53. Based on median results, population rate of growth was greater in the contemporary period as compared to the historic period (historic: $\lambda = 1.01$; contemporary: $\lambda = 1.11$).

Modeling results were similar to estimated female lifetime productivity values (Table 4), although productivity values suggested that female black bears from 1984–1991 might not be reproducing at a high enough rate (0.73; 90% CI = 0.26–1.72) to replace themselves (Table 4). Changing age of reproductive senescence to 18 years (an age which females were believed to be

Table 4.2. Initial population size, survival rates (SE), and recruitment rates (SE) used in stochastic population simulation models for 10 year simulations of population growth of black bears during historic (1984–1991) and contemporary (2003–2006) periods in Rocky Mountain National Park, Colorado.

	Historic			Contemporary		
	Initial pop size	Survival	Recruitment	Initial pop size	Survival	Recruitment
Females	4.6	95.0 (3.0)	34.0 (8.0)	6.3	95.0 (3.0)	56.0 (14.0)
Males	5.5	91.7 (6.8)		6.3	91.7 (6.8)	
Subadults	11.9	74.5 (20.5)		9.4	83.4 (13.6)	

Table 4.3. Percent probability of black bear population size exceeding estimated levels after 10 years based on 1,000 stochastic population simulations using demographic data for historic (1984–1991) and contemporary (2003–2006) periods in Rocky Mountain National Park, Colorado. Median population size is in bold.

Historic		Contemporary	
% probability	Population size	% probability	Population size
100	12	100	41
90	19	90	53
80	21	80	56
70	23	70	59
60	24	60	61
50	**25**	**50**	**63**
40	26	40	65
30	27	30	67
20	29	20	70
10	31	10	74
0	38	0	92

Table 4.4. Female (F) black bear reproductive parameters for historic (1984–1991) and contemporary (cont, 2003–2006) periods in Rocky Mountain National Park (RMNP), Colorado, as well as mean values for the western U.S. All values are means and include age of primiparity (prim), litter interval, litter size, cub survival (surv), natality (cubs/female/year), recruitment (yearlings/female/year; recruit), number of years a female was reproductively active (years), number of females recruited per female reproductive lifetime (F recruit × years), annual subadult female (SAF) survival, SAF survival to age of reproduction (SAF surv to adult), and the number of female cubs reaching reproductive age/female reproductive lifetime (F prod).

	Age of prim	Litter interval	Litter size	Cub surv	Natality	Recruit	Years	F recruit × years	SAF surv	SAF surv to adult	F prod
RMNP historic	7.5	2.25[a]	1.78	0.43	0.79	0.34	7.5	1.28	0.92	0.57	0.73
RMNP cont	5.5[b]	2.25[c]	1.75	0.71	0.78	0.56	9.5	2.66	0.92	0.68	1.80
Western U.S.	5.2[d]	2.60[e]	1.76[f]	0.72[g]	0.74[e]	0.60[h]	9.8[d]	2.98[h]	0.86[i,j]	0.53[j]	1.58[j]

[a] litter intervals were not provided so estimates from contemporary data set were used.

[b] included an estimated age of first reproduction for 1 subadult who had not reproduced by the end of data collection.

[c] included litter intervals estimated for 2 females but were not verified due to the end of data collection.

[d] values obtained from: Beck 1991, Beecham 1980, Costello et al. 2001, Frost 1990, Goodrich 1990, Jonkel and Cowan 1971, Kasworm and Their 1994, Tolman 1998, T. Wertz personal communication.

[e] values obtained from: Beck 1991, Beecham 1980, Costello et al. 2001, Frost 1990, Goodrich 1990, Jonkel and Cowan 1971, Kasworm and Their 1994, Keay 1995, Piekielek and Burton 1975, Tolman 1998, T. Wertz personal communication.

[f] values obtained from: Beck 1991, Beckmann and Berger 2003b, Beecham 1980, Costello et al. 2001, Frost 1990, Goodrich 1990, Jonkel and Cowan 1971, Kasworm and Manley 1988, Kasworm and Their 1994, Keay 1995, Piekielek and Burton 1975, Rohlman 1989, Rosgaard and Simmons 1982, Tolman 1998, T. Wertz personal communication.

[g] values obtained from: Beck 1991, Beckmann and Berger 2003b, Costello et al. 2001, Frost 1990, Jonkel and Cowan 1971, Tolman 1998, T. Wertz personal communication.

[h] values obtained from: Beck 1991, Costello et al. 2001, Frost 1990, Jonkel and Cowan 1971, Tolman 1998, T. Wertz personal communication.

[i] included an estimate from Frost (1990) for all females combined; little difference was noted between adults and subadults.

[j] values obtained from: Beck 1991, Costello et al. 2001, Frost 1990.

reproductively active in RMNP; RMNP, unpublished data) increased the number of female cubs reaching reproductive age/female reproductive lifetime to 1.02 (90% CI = 0.35–2.42). Lifetime reproductive success of females during the 2003–2006 period was 1.80 (90% CI = 0.75–3.49), similar to other values seen in most western U.S. black bear populations (Table 4).

DISCUSSION

Productivity of black bears in the contemporary period in RMNP was higher than observed historically, primarily because of higher recruitment rates resulting from increased cub survival and a reduction in age of first reproduction, which are the 2 population parameters first influenced by changes in maternal condition in large mammals (Gaillard et al. 2000, Eberhardt 2002). Cub survival has been implicated as a primary factor regulating black bear populations (Fuller 1993, Powell et al. 1996). The rate of cub survival observed from 1984–1991 in RMNP was among the lowest recorded for black bears (Garshelis 1994), though contemporary levels were similar to other populations throughout the western U.S. (Table 4). Although causes of mortality were unknown for most cubs for both time periods, starvation and infanticide were observed during the historical period (McCutchen 1993). Because infanticide is seen to some extent in most black bear populations (e.g., LeCount 1987), a change in nutritional condition was likely the primary factor behind increased cub survival seen in the contemporary period. Adult females were larger (weight = 68 [SE = 6] kg) with higher levels of body fat (23% [SE = 5]) during the summer season than historically (weight = 60 [SE = 5] kg, body fat = 15% [SE = 2]; see Chapter 2). Additionally, 2 pregnant females were in very good condition at early hibernation during the contemporary period (body fat = 36 and 34% for each bear, respectively).

Cub survival varies geographically (Beck 1991, Noyce and Garshelis 1994) with maternal condition hypothesized to influence cub survival when it drops below a certain threshold (Elowe and Dodge 1989, Noyce and Garshelis 1994). This threshold may vary depending on mean size of female black bears but is usually only observed with females in very poor condition (Minnesota = 65 kg, Noyce and Garshelis 1994). The small size (60 kg) and lower condition (15% body fat) of black bears historically suggests these reproductive females may have often been close to or below such a threshold level. Low yearling weights ($\bar{x}$ = 12 kg; McCutchen 1993) during the historic period provide further evidence of this, as light-weight females are more likely to produce light-weight yearlings (Garshelis 1994, Noyce and Garshelis 1994). Further, weights close to 10 kgs can predispose yearlings to increased mortality (Noyce and Garshelis 1994), and yearling survival (0.70, Zeigenfuss 2001) was low for black bears in RMNP during the historic period compared to adjacent populations (i.e., west-central Colorado = 0.94, Beck 1991). Thus, increased nutritional condition of black bears in RMNP likely resulted in increased bear productivity observed in 2003–2006, regardless of whether increases were due to incremental increases in black bear condition or exceeding critical thresholds.

Predation and infanticide also likely influenced cub survival in RMNP. The 2 known cubs that died during the contemporary period were harassed by coyotes (*Canis latrans*) on multiple occasions and were in close proximity to a large male not believed to have sired them (R. Baldwin and L. Bender, unpublished data). However, although the cubs appeared healthy, the mother was in poorer condition (summer body fat = 14%) than other females in RMNP, so I cannot conclusively exclude malnutrition as the cause of mortality. Although nutritional condition may have a dominant effect on cub survival, survival can also be influenced by density-independent factors and other factors independent of maternal condition (Gaillard et al. 2000).

Later onset of reproduction reduces the number of years a female is reproductively active, thereby reducing the number of breeding opportunities. Additionally, later age of primiparity decreases the likelihood a female will survive to reproductive age. Although my data on age of primiparity were limited, the early reproductive age of 1 female (4 years) from the contemporary period was reflective of good body condition (early hibernation: weight = 94 kg, body fat = 34%), as age of first reproduction is influenced by body size and presumably absolute condition (Beecham 1980, Rogers 1976, 1987, Kolenosky 1990, Beck 1991, Samson and Huot 1995). Later reproduction was noted for the other primiparous female observed from 2003–2006. However, this female resided almost exclusively in wildland areas and was consistently in poorer shape (early hibernation weight = 67 kg, body fat = 22%), whereas the earlier reproducing female was frequently located in heavy human-use areas (see Chapter 7). This proximity to human-use areas likely resulted in greater consumption of anthropogenic foods by the earlier reproducing female (see Chapter 6), thus increasing habitat potential of the landscape to levels greater than those associated solely with natural foods, as black bear condition in RMNP was positively related to use of human-use areas (see Chapter 7). The later reproducing female lacked this dietary supplementation and utilized similar habitats as those present for the 2 primiparous females from the historical study period, with age of primiparity similar among the 3 individuals (7, 8, and 7 years, respectively). Increased nutrition for nulliparous females, associated with use of human-derived foods (see Chapters 5, 6, and 7), will likely reduce the age of primiparity for black bears in RMNP and could lead to much greater cub production in the future. A similar scenario was observed in the Lake Tahoe region of Nevada (Beckmann and Berger 2003b) and further supports the sensitivity of reproduction to nutritional condition.

Litter size varied little between contemporary and historic data in RMNP and was similar to other values for Colorado and the West (Table 4). Litter size appears to be less sensitive to maternal condition although conclusions vary by study (McDonald and Fuller 2001). Noyce and Garshelis (1994) noted that the effect of maternal condition on litter size in Minnesota was an artifact of primiparous vs. multiparous mothers, as first litters were usually smaller than subsequent litters. They suggested that pooling of first and subsequent litters can influence the relationship between litter size and body weight and may have influenced the positive trends observed for this relationship in other studies (i.e., Kolenosky 1990, Stringham 1990). However, age was controlled for in a Nevada study and still indicated larger litter size with increased maternal condition (Beckmann and Berger 2003b). Similarly, black bears of very high weights in Pennsylvania and Minnesota were noted to produce exceptionally large litters (i.e., 4–5 cubs, Alt 1989, Noyce and Garshelis 1994). Possibly, substantial increases in litter size require that condition must approach maximum values. Maximum condition levels for black bears are unknown, and females in RMNP showed levels of condition (body fat = 23%; see Chapter 2) that were higher than historic levels (body fat = 15%; see Chapter 2) without an increase in litter size. Thus, it is possible that it is absolute size that influences litter size more than relative condition, particularly given that most previous work used mass to index condition.

I was unable to assess changes in interbirth interval as such data were unavailable from the historic period. In the contemporary period, black bears in RMNP exhibit comparable or slightly shorter intervals compared to other western U.S. populations. Although long intervals can reduce natality and subsequent reproductive output of black bear populations (i.e., Jonkel and Cowan 1971), interbirth interval appears to be the last reproductive parameter affected by condition (Noyce and Garshelis 1994) and likely had little effect on the variability in cub production between sample periods in RMNP.

Simulation of black bear populations in RMNP reflected increased population productivity for the contemporary population resulting in greater population rate of increase (historic: $\lambda = 1.01$; contemporary: $\lambda = 1.11$). This increase resulted from greater recruitment to the yearling age-class (influenced by cub survival), as well as earlier onset of reproduction. Earlier onset of reproduction can have several potential effects on productivity, including a decrease in the proportion of subadults in the population (see above), increased years of reproductive activity (Table 4), and increased number of females reaching the age of first reproduction (Table 4). Therefore, even though annual survival of subadult females was equal between study periods in RMNP, greater numbers reached the reproductive age class during the contemporary period due to earlier age of primiparity and greater rate of population increase.

Despite low productivity, the historic black bear population in RMNP was likely able to maintain numbers without significant immigration because of high adult survival (no documented mortalities of collared individuals during this time). Survival of adult females has the greatest elasticity on population rate of increase (Gaillard et al. 2000, Freedman et al. 2003), meaning that even slight changes can cause large fluctuations in population growth. However, survival of adults tends to vary little annually (Gaillard et al. 2000); this would be especially true in protected areas such as RMNP, where adult survival rates should be near maximum unless habitat condition was extremely poor. This protection was particularly important historically, as adult female survival is the primary factor influencing population dynamics of bears (black bears—Freedman et al. 2003, brown bears [*Ursus arctos*]—Eberhardt 1990, Wielgus et al. 2001, polar bears [*Ursus maritimus*]—Taylor et al. 1987, Eberhardt 1990) due to its influence on cubs and cub survival (Bunnell and Tait 1981, 1985, McLellan and Shackleton 1988, Mykytka and Pelton 1990, Hellgren and Maehr 1993, but see Gaillard et al. [1998, 2000] for discussion on temporal variation). Without these high survival rates, productivity would have been too low for black bears to persist in RMNP historically without significant immigration, especially given early onset of reproductive senescence (Table 4). The increase in productivity of black bears to levels typical of other western populations (Table 4) currently seen in RMNP, in combination with continued high survival, has resulted in high potential for the contemporary black bear population to grow substantially based on current demographics (Table 3). However, because much of the increase in productivity may be associated with enhanced nutrition associated with increased use of human-interface habitats, mortality rates may increase in the future due to increased human-bear conflicts. Continued monitoring of the current black bear population (see Chapter 3) will be necessary to see whether this occurs and whether increased mortality rates negate increased productivity.

MANAGEMENT IMPLICATIONS

Historically, black bear populations in RMNP were among the least productive in North America. However, contemporary data indicates productivity equivalent to other populations in the western U.S. This increased productivity may be related to nutritional supplementation from anthropogenic foods in and adjacent to RMNP, as contemporary consumption of human foods has increased by a minimum of 15 fold over historic levels. Additionally, both size and condition of black bears has increased from historic levels, providing an indication of enhanced nutrition (see Chapter 6), and bear condition is positively associated with use of human-use areas in RMNP (see Chapter 7). Historically, black bears in RMNP ostensibly exhibited cryptic behavior and avoided heavy human-use areas (McCutchen 1990). However, continued development along the boundary of RMNP and increased visitor use has increased the potential for human-bear encounters (Zeigenfuss 2001). Many black bears in the contemporary population no longer exhibit this avoidance of human-use areas, with home-ranges including many human-use areas (see Chapter 7). A similar situation was observed in the Lake Tahoe region of Nevada (Beckmann and Berger 2003a, b). Although increased productivity initially appears positive, it may be offset by increased mortality from bear-human encounters. For example, use by black bears of human-interface areas may lead to greater vehicular collisions (Beckmann and Berger 2003b, Freedman et al. 2003) and will likely increase negative bear-human encounters (Peirce and Van Daele 2006), possibly leading to the destruction of problem individuals. One such encounter was noted during this study, as the first human attack by a black bear in RMNP since 1971 occurred in 2003, with this bear subsequently euthanized. Additionally, following the conclusion of this study, a formerly radio-collared individual was euthanized for repeated damage to property. Improvements of natural foods and habitats, such as derived from prescribed burning, “let burn” wildfire management, or other habitat manipulations, could provide a sustainable strategy for increasing black bear productivity while minimizing bear-human conflicts. Conflicts may also increase in the future given that black bears in RMNP show a high potential of increasing in numbers, which also increases the likelihood of black bears persisting in RMNP. Fundamentally, black bear numbers will still be strongly affected, and possibly limited, by the influence of climate, particularly because of limitations associated with hot, dry years (see Chapter 1). Increased use of human-associated areas and foods, however, has the potential to decouple the RMNP black bear population from such natural climatic limitations.

LITERATURE CITED

Alt, G. L. 1984. Black bear cub mortality due to flooding of natal dens. Journal of Wildlife Management 48:1432–1434.

Alt, G. L. 1989. Reproductive biology of female black bears and early growth and development of cubs in northeastern Pennsylvania. Dissertation, West Virginia University, Morgantown, West Virginia, USA.

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

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

Beecham, J. J. 1980. Some population characteristics of two black bear populations in Idaho. International Conference on Bear Research and Management 4:201–204.

Bender, L. C., G. J. Roloff, and J. B. Haufler. 1996. Evaluating confidence intervals for habitat suitability models. Wildlife Society Bulletin 24:347–352.

Bender, L. C., G. A. Schirato, R. D. Spencer, K. R. McAllister, and B. L. Murphie. 2004. Survival, cause-specific mortality, and harvesting of male black-tailed deer in Washington. Journal of Wildlife Management 68:870–878.

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

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.

Bunnell, F. L., and D. E. N. Tait. 1981. Population dynamics of bears—implications. Pages 75–98 *in* C. W. Fowler and T. D. Smith, editors. Dynamics of large mammal populations. John Wiley and Sons, New York, New York, USA.

Bunnell, F. L., and D. E. N. Tait. 1985. Mortality rates of North American bears. Arctic 38:316–323.

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, New Mexico, USA.

Costello, C. M., D. E. Jones, R. M. Inman, K. H. Inman, B. C. Thompson, and H. B. Quigley. 2003. Relationship of variable mast production to American black bear reproductive parameters in New Mexico. Ursus 14:1–16.

Eberhardt, L. L. 1990. Survival rates required to sustain bear populations. Journal of Wildlife Management 54:587–590.

Eberhardt, L. L. 2002. A paradigm for population analysis of long-lived vertebrates. Ecology 83:2841–2845.

Eiler, J. H., W. G. Wathen, and M. R. Pelton. 1989. Reproduction in black bears in the southern Appalachian Mountains. Journal of Wildlife Management 53:353–360.

Elowe, K. D., and W. E. Dodge. 1989. Factors affecting black bear reproductive success and cub survival. Journal of Wildlife Management 53:962–968.

Freedman, A. H., K. M. Portier, and M. E. Sunquist. 2003. Life history analysis for black bears (*Ursus americanus*) in a changing demographic landscape. Ecological Modelling 167:47–64.

Frost, H. C. 1990. Population and reproductive characteristics of black bears on an isolated mountain in southeastern Utah. Thesis, Brigham Young University, Provo, Utah, USA.

Fuller, D. P. 1993. Black bear population dynamics in western Massachusetts. Thesis, University of Massachusetts, Amherst, Massachusetts, USA.

Gaillard, J.-M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology and Evolution 13:58–63.

Gaillard, J.-M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toïgo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31:367–393.

Garshelis, D. L. 1994. Density-dependent population regulation of black bears. Pages 3–14 *in* M. Taylor, editor. Density-dependent population regulation in black, grizzly, and polar bears. International Conference on Bear Research and Management Monograph Series No. 3.

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. 1990. Ecology, conservation and management of two western Great Basin black bear populations. Thesis, University of Nevada Reno, Reno, Nevada, USA.

Gunther, K. A., M. J. Biel, N. Anderson, and L. Waits. 2002. Probable grizzly bear predation on an American black bear in Yellowstone National Park. Ursus 13:372–374.

Harlow, H. J., T. Lohuis, R. G. Grogan, and T. D. I. Beck. 2002. Body mass and lipid changes by hibernating reproductive and nonreproductive black bears (*Ursus americanus*). Journal of Mammalogy 83:1020–1025.

Heisey, D. M., and T. K. Fuller. 1985. Evaluation of survival and cause specific mortality rates using telemetry data. Journal of Wildlife Management 49:668–674.

Hellgren, E. C., and D. S. Maehr. 1993. Habitat fragmentation and black bears in the eastern United States. Proceedings of the Eastern Workshop on Black Bear Research and Management 11:154–165.

Jonkel, C. J., and I. McT. Cowan. 1971. The black bear in the spruce-fir forest. Wildlife Monographs 27.

Kasworm, W. F., and T. Manley. 1988. Grizzly bear and black bear ecology in the Cabinet Mountains of Northwest Montana. Montana Department of Fish, Wildlife, and Parks, Helena, Montana, USA.

Kasworm, W. F., and T. J. Their. 1994. Adult black bear reproduction, survival, and mortality sources in northwest Montana. International Conference on Bear Research and Management 9:223–230.

Keay, J. A. 1995. Black bear reproductive rates in Yosemite National Park. California Fish and Game 81:122–131.

Kemp, G. A. 1976. The dynamics and regulation of black bear *Ursus americanus* populations in northern Alberta. International Conference on Bear Research and Management 3:191–197.

Kolenosky, G. B. 1990. Reproductive biology of black bears in east-central Ontario. International Conference on Bear Research and Management 8:385–392.

LeCount, A. L. 1987. Causes of black bear cub mortality. International Conference on Bear Research and Management 7:75–82.

Mattson, D. J., R. R. Knight, and B. M. Blanchard. 1992. Cannibalism and predation on black bears by grizzly bears in Yellowstone ecosystem, 1975–1990. Journal of Mammalogy 73:422–425.

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.

McCutchen, H. E. 1993. Ecology of high mountain black bear population in relation to land use at Rocky Mountain NP. Park Science 13:25–27.

McDonald, J. E., Jr., and T. K. Fuller. 2001. Prediction of litter size in American black bears. Ursus 12:93–102.

McLellan, B. N., and D. M. Shackleton. 1988. Grizzly bears and resource-extraction industries: effects of roads on behavior, habitat use and demography. Journal of Applied Ecology 25:451–460.

Mykytka, J. M., and M. R. Pelton. 1990. Management strategies for Florida black bears based on home range habitat composition. International Conference on Bear Research and Management 8:161–167.

Noyce, K. V., and D. L. Garshelis. 1994. Body size and blood characteristics as indicators of condition and reproductive performance in black bears. International Conference on Bear Research and Management 9:481–496.

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.

Peirce, K. N., and L. J. Van Daele. 2006. Use of a garbage dump by brown bears in Dillingham, Alaska. Ursus 17:165–177.

Pelton, M. R. 2000. Black bear. Pages 389–408 *in* S. Demarais and P. R. Krausman, editors. Ecology and management of large mammals in North America. Prentice-Hall, Upper Saddle River, New Jersey, USA.

Pelton, M. R. 2003. Black bear (*Ursus americanus*). Pages 547–555 *in* G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, editors. Wild mammals of North America: biology, management, and conservation. Second edition, revised. The Johns Hopkins University Press, Baltimore, Maryland, USA.

Piekielek, W., and T. S. Burton. 1975. A black bear population study in northern California. California Fish and Game 61:4–25.

Pollock, K. H., S. R. Winterstein, C. M. Bunch, and P. D. Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. Journal of Wildlife Management 53:7–15.

Powell, R. A., J. W. Zimmerman, D. E. Seaman, and J. F. Gilliam. 1996. Demographic analysis of a hunted black bear population with access to a refuge. Conservation Biology 10:224–234.

Rogers, L. L. 1976. Effects of mast and berry crop failures on survival, growth, and reproductive success of black bears. Transactions of the North American Wildlife and Natural Resource Conference 41:431–438.

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.

Rohlman, J. A. 1989. Black bear ecology near Priest Lake, Idaho. Thesis, University of Idaho, Moscow, Idaho, USA.

Rosgaard, A., and C. Simmons. 1982. East Boulder big game technical report. Montana Department of Fish, Wildlife and Parks, Helena, Montana, USA.

Samson, C., and J. Huot. 1995. Reproductive biology of female black bears in relation to body mass in early winter. Journal of Mammalogy 76:68–77.

Schwartz, C. C., and A. W. Franzmann. 1991. Interrelationship of black bears to moose and forest succession in the northern coniferous forest. Wildlife Monographs 113.

Schwartz, C. C., and A. W. Franzmann. 1992. Dispersal and survival of subadult black bears from the Kenai Peninsula, Alaska. Journal of Wildlife Management 56:426–431.

Sorensen, V. A., and R. A. Powell. 1998. Estimating survival rates of black bears. Canadian Journal of Zoology 76:1335–1343.

Stringham, S. F. 1990. Black bear reproductive rate relative to body weight in hunted populations. International Conference on Bear Research and Management 8:425–432.

Taylor, M. K., D. P. DeMaster, G. L. Bunnell, and R. E. Schweinsburg. 1987. Modeling the sustainable harvest of female polar bears. Journal of Wildlife Management 51:811–820.

Tolman, J. 1998. A comparison of reproductive and habitat characteristics of two Utah black bear populations. Thesis, Brigham Young University, Provo, Utah, USA.

Wielgus, R. B., F. Sarrazin, R. Ferriere, and J. Clobert. 2001. Estimating effects of adult male mortality on grizzly bear population growth and persistence using matrix models. Biological Conservation 98:293–303.

Zeigenfuss, L. C. 2001. Ecology of black bears in Rocky Mountain National Park: an analysis of population dynamics, diet, and habitat selection (1985–1991). Unpublished report, U.S. National Park Service, Rocky Mountain National Park, Colorado.

Chapter 5:

Den-site characteristics and denning chronology of black bears in Rocky Mountain National Park, Colorado

Roger A. Baldwin, Department of Animal and Range Sciences, New Mexico State University, P.O. Box 30003 MSC 4901, Las Cruces, New Mexico 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, New Mexico 88003, USA

Chapter summary: Hibernation is an important physiological process for black bears (*Ursus americanus*) in temperate North America, and thus dens are key habitat components for managers. We compared historic (1984–1991) and contemporary (2003–2006) den locations for habitat and physiographic attributes and used maximum entropy modeling to determine habitat factors most influential in predicting den-site locations. Additionally, we determined den entrance and emergence dates for black bears and related these dates to productivity, climatic, and demographic factors to assess their influence on denning chronology. We observed a shift in the relationship between den locations and most habitat and physiographic factors (aspect, elevation, covertype, distance to roads and trails) over time. Best supported models of den locations differed between historic (slope, elevation, covertype) and contemporary periods (slope, distance to roads, aspect, canopy height). In general, den locations were shifting toward areas closer to human developments. Date of den entrance appeared to be most strongly influenced by age class and correlates of primary productivity (growing-season precipitation and temperature), with den entrance typically later for adult black bears during cooler, wetter years. Although sex was loosely correlated to den exit (males emerged before females), we found no meaningful results for other correlates.

Hibernation is an essential component of the black bear (*Ursus americanus*) lifecycle throughout most of its geographical range with dens providing shelter and protection during this period (Rogers 1987, Beck 1991, DeGayner et al. 2005). Identifying factors affecting den-site selection is important for wildlife managers to provide for this critical habitat attribute. Biologists believed that lack of appropriate den sites might have been limiting the black bear population in Rocky Mountain National Park, Colorado (RMNP; Zeigenfuss 2001). Because number of black bears in RMNP is low (< 24 individuals; Chapter 3), identifying factors important in 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 habitat correlates (e.g., Johnson and Pelton 1981, Oli et al. 1997, Zeigenfuss 2001). This approach assumes sites are classed correctly as used/not used (MacKenzie et al. 2002, Anderson 2003). However, random sites may well have been used by black bears in previous seasons, may simply not be used because of absence of black bears in the area, or may be used by unmarked black bears; there is no certainty that they in fact were not suitable for denning. Recently, analytical techniques (e.g., maximum entropy; Phillips et al. 2006) have been developed that utilize only known locations to identify habitat correlates and are therefore free from potential biases of approaches that utilize randomly selected absence locations (Anderson 2003, Phillips et al. 2006). Such approaches should allow much more confident identification of what habitat correlates are actually associated with den sites.

Understanding the factors that influence the timing and duration of denning also provides valuable insight for black bear management. It is generally accepted that reduction in photoperiod and temperature associated with late autumn and early winter provides the initial cue for denning (Johnson and Pelton 1980, Schooley et al. 1994). However, the ultimate factor influencing denning dates likely relates to energy balance of the individual bear (Lindzey and Meslow 1976, Elowe 1984, Schooley et al. 1994). As food becomes scarce, a negative energy balance occurs, and because it is no longer advantageous to continue foraging, bears den. Therefore, in much of the black bear's range, food availability is likely a strong predictor of the denning period (Johnson and Pelton 1980, Tietje and Ruff 1980, Beecham et al. 1983, Schooley et al. 1994, Costello et al. 2001). Unfortunately, reliable measures of food availability are often unavailable. Conversely, climatic data such as temperature and precipitation have been correlated to vegetative production (e.g., Koehler and Pierce 2003), are readily available, and provide a possible alternative for assessing this relationship. Likewise, the timing of den emergence is also influenced by multiple factors including snowmelt (Rogers 1987, Schoen et al. 1987, Schwartz et al. 1987), temperature (Lindzey and Meslow 1976, O'Pezio et al. 1983, Kolenosky and Strathearn 1987, Rogers 1987), and sex and age class of individuals (Novick et al. 1981, LeCount 1983, Rogers 1987), and consequently appears to vary substantially across locations.

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 and proximate factors affecting denning chronology may be necessary to maintain a viable black bear population. Knowing factors affecting den-site selection allows Park managers to ensure that these components are present on the RMNP landscape. Similarly, knowing what triggers denning chronology, especially if related to food, allows staff to address habitat attributes important to black bear energetics and thus productivity in RMNP. Consequently, my objectives were to: 1) determine habitat attributes that best predict suitable denning habitat both currently and historically in RMNP; and 2) determine which factors best predict den entrance and emergence of black bears in RMNP.

METHODS

Capture and telemetry

I used modified Aldrich foot snares and culvert traps to capture black bears from 1984–1991 (historic period) and 2003–2006 (contemporary period). I immobilized bears with a 5:1 mixture of ketamine hydrochloride and xylazine hydrochloride (200 mg ketamine and 40 mg xylazine per ml) and fit bears with radiocollars to facilitate location of den sites. I also placed bears into appropriate sex and age categories (subadult vs. adult); adult females were differentiated from subadults based on known age, nipple size, and nipple coloration (Beck 1991, Brooks and McRoberts 1997), while adult males were identified by larger size, obvious staining of teeth, and descended testicles (Beck 1991, Garshelis and Hellgren 1994).

Starting 1 October, I typically located bears ≥ 2 times weekly to determine date of den entrance; bear locations were checked periodically starting 1 March to determine date of den exit. I assigned an approximate date of den entrance equal to the median date between the last known date of activity and the first date of known denning and vice versa for den exit. Den sites were either plotted on maps and converted to UTM coordinates or recorded using a GPS unit.

Denning habitat

I 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 class and was coded as: 0 = no canopy, 1 = < 1 m, 2 = 1–5 m, 3 = 5–15 m, 4 = 15–30 m, and 5 = > 30 m. I measured slope from 0º–90º, and recorded elevation to the nearest meter. I classed aspect as: north = 316º–45º, east = 46º–135º, south = 136º–225º, and west = 226º–315º. I also measured the distance to nearest road (m) and trail (m). I extracted all habitat attribute data from GIS layers of RMNP and surrounding areas using ArcView 3.3 (Environmental Systems Research Institute, Redlands, California, USA).

I used *t*-tests (Zar 1999) to compare differences in distance to roads and trails, elevation, and slope between den sites from the historic and contemporary periods. I used Mann–Whitney *U*-tests (Zar 1999) to assess differences in canopy height and contingency tables (Zar 1999) to test for differences in covertype and aspect between the 2 periods. I used only the actual

Table 5.1. Description of covertypes used to assess black bear den distribution in Rocky Mountain National Park, Colorado.

Covertype	Description
Herbaceous upland	Dry, open meadows
Herbaceous wetland	Herbaceous communities found on wetland or marshy sites
Shrub riparian cross zone	Shrublands lining streambanks and valley bottoms
Shrub upland lower montane	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/fir species along riparian or seasonally flooded areas
Mixed conifer	Characterized by codominance of 2 or more 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 can be codominant
Rock	Characterized by rock, bare soil, or snow
Open water	Lakes and reservoirs
Non-vegetated surface	Included areas covered by roads, trails, and campsites

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) to facilitate estimation due to small sample sizes. Furthermore, because all den sites from the contemporary period were located east of the continental divide, I conducted these same tests between east and west-side den sites for historic dens to see if differences between periods were due to the inclusion of den sites west of the continental divide.

I modeled den locations using Maximum Entropy 2.3 (Phillips et al. 2006) to predict areas in RMNP with suitable denning habitat. This approach utilizes only known locations to determine important habitat attributes, thereby eliminating the need for absence data (Phillips et al. 2004, 2006), and provides a less biased alternative to other approaches that require the generation of non-den locations (i.e., discriminant analysis; Johnson and Pelton 1981, Oli et al. 1997). I used all previously listed variables for this analysis and constructed separate models for historic and contemporary periods.

I 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 while specificity provides a measure of correctly predicted absences (Fielding and Bell 1997). I also used the area under curve (AUC) approach to assist in selecting the most appropriate model (Fielding and Bell 1997, Phillips et al. 2006). This approach provides an index of model accuracy; values range from 0.5–1.0 with values of 0.5 indicating no fit greater than that expected by chance. Standard errors were calculated for AUC values using 30% of the den sites as test data (Phillips et al. 2006). Often, AUC values are greatest for models with many variables, though certain variables may add little to the model. Therefore, I used a critical ratio test (Pearce and Ferrier 2000) to compare the most general model (containing all variables) to simpler models to determine if the increase in explanatory value was significant at $\alpha = 0.05$. Because models were constructed using the same evaluation data, Spearman rank correlation coefficients (r_s) were calculated between competing models. In contrast to Pearce and Ferrier (2000), I could only construct correlations for known den locations as I lacked absence data. Spearman correlation coefficients were then related to the table provided by Hanley and McNeil (1983) to derive r and were incorporated into the critical ratio test (Pearce and Ferrier 2000) using the following:

$$Z = \frac{A_1 - A_2}{\sqrt{SE_{A_1}^2 + SE_{A_2}^2 - 2r\,SE_{A_1} SE_{A_2}}}$$

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, I selected the more parsimonious model as my preferred model.

Additionally, I 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). I used these thresholds to convert probabilities to binary responses (presence-absence). For my study, I used the equal test sensitivity and specificity threshold and used these threshold values to calculate classification percentages 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 relationship, and the magnitude of these movements indicates the strength of these relationships. Finally, I mapped the change in selected denning habitats between the historic and contemporary periods to illustrate shifts in den locations.

Denning chronology

I analyzed denning chronology only on data from 2003–2006 for den entrance and 2004–2006 for den exit as no data was available from 1984–1991. I used linear regression (Ramsey and Shafer 1997) to relate sex, age class, precipitation (cm), maximum temperature (ºC), and elevation (m) to date of den entrance (Julian date) to assess their influence on denning chronology with sex (male = 0, female = 1) and age class (adult = 0, subadult = 1) treated as indicator variables in the analyses (Ramsey and Shafer 1997). I obtained precipitation and temperature values recorded from 1 April–30 September in Estes Park (http://weather-source.com) and 2 additional sites in RMNP (http://www.wcc.nrcs.usda.gov/snow) and used the average of these values in analyses. I used precipitation and temperature values recorded over this time-frame as a surrogate for vegetative productivity for each respective year as both are closely tied to herbaceous production (Koehler and Pierce 2003). Additionally, elevation was recorded at all den sites as I believed earlier denning bears might utilize higher den locations. I assessed outliers using residual plots and compared models using R^2 for univariate models and adjusted R^2 values for multivariate models as all models had similar number of parameters (Ramsey and Schafer 1997).

Inspection of data suggested 2 distinct subgroups based on date of den entrance: 1) early (12 October–6 November) and 2) late (16–27 November). I used logistic regression (Hosmer and Lemeshow 2000) to relate sex, age class, precipitation, temperature, and elevation to these subgroups to determine their influence on probability of early or late denning. I considered only models with ΔAIC's < 4 as competing models (Burnham and Anderson 1998), and further used rescaled generalized R^2 values and concordance in determining model fit (Nagelkerke 1991, Eberhardt 2003). I calculated odds ratios to facilitate interpretation of variables. I also used linear regressions to estimate den entrance based on these same factors for early and late denning periods and analyzed models as above.

I also used linear regression to relate sex, age class, maximum temperature, snowpack, and elevation to date of den exit. Here, temperature represented the mean maximum temperature for March–April, and was recorded at the same locations as those used in den entrance analyses. I obtained snowpack from 4 snow course sites in RMNP for March–April (http://www.wcc.nrcs.usda.gov/cgibin/state-site.pl?report=snowcourse) and used the mean in analyses. I selected this time frame to represent temperature and snowpack immediately prior to and subsequent to typical den emergence (i.e., mid to late April). I analyzed data identically to den entrance.

RESULTS

Denning habitat

I obtained 35 den locations for 1984–1991 and 22 locations for 2003–2006. Although the specific type of den was not known for all den sites from 1984–1991, 21 were rock dens, 2 were tree dens, and 1 was dugout; I observed only rock dens in 2003–2006. Contemporary dens were closer to roads ($t = 2.2$, df = 55, $P = 0.029$) and trails ($t = 1.8$, df = 55, $P = 0.076$), lower in elevation ($t = 2.4$, df = 55, $P = 0.021$; Table 2), more varied in covertype ($\chi^2_5 = 13.1$, $P = 0.023$), and less varied in aspect ($\chi^2_3 = 7.1$, $P = 0.069$) than historic sites (Table 3). Differences between periods were not due to inclusion of west-side dens in historic data, as only aspect differed ($\chi^2_3 = 9.8$, $P = 0.020$) between east and west-side den locations (Tables 3 and 4).

The best models for each subset of parameters (2–7) varied between historic and contemporary periods (Table 5). AUC values differed significantly between the most general model and several of the simpler models (Table 5), so I excluded these models from further consideration. Additionally, derived classification percentages for each model indicated some were substantially more efficient than others (Table 5). Based on these criteria, I selected the model containing slope, elevation, and covertype as the preferred model for 1984–1991 dens because of parsimony given relatively equivalent AUC scores and classification percentages (Fig. 1). Response curves indicated increased probability of use for den sites was associated with greater slopes, higher elevations peaking at 3,100 m, and dead and down, mixed conifer, lodgepole pine, Douglas fir, and herbaceous upland covertypes (Fig. 2).

I selected the model containing slope, aspect, distance to roads, and canopy height as preferred for 2003–2006 dens given its high AUC and classification values compared to higher order models (Fig. 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. 4). The shift in selected denning habitats between the studies illustrates a movement from more remote areas to locations of heavier human-use in RMNP (i.e., closer to roads and developed areas; Fig. 5)

Table 5.2. Comparisons between black bear den locations and selected variables from 1984–1991 and 2003–2006 in Rocky Mountain National Park, Colorado.

	1984–1991 (n = 35)		2003–2006 (n = 22)			
Variable	$\bar{x}$	SE	$\bar{x}$	SE	t	P
distance to roads (m)	2,555	299	1,648	186	2.2	0.029
distance to trails (m)	1,127	150	746	115	1.8	0.076
elevation (m)	3,114	26	2,995	49	2.4	0.021
slope (°)	27.5	1.4	25.1	1.8	1.1	0.298
canopy height (m)[a]	9.7	0.7	9.3	0.5	0.3	0.765

[a] Mean scores and standard errors were obtained by using the median height value for each assigned class and are presented only for comparative purposes. The statistic and associated *P*-value were derived using the Mann–Whitney *U*-test.

Table 5.3. Comparisons between black bear den locations and selected variables for eastern and western localities from 1984–1991 in Rocky Mountain National Park, Colorado.

	Eastern ($n = 21$)		Western ($n = 14$)			
Variable	$\bar{x}$	SE	$\bar{x}$	SE	t	P
distance to roads (m)	2,352	321	2,859	578	–0.8	0.414
distance to trails (m)	1,179	171	1,050	283	0.4	0.416
elevation (m)	3,097	34	3,139	39	–0.8	0.423
slope (°)	29.1	2.0	25.2	1.9	1.3	0.190
canopy height (m)[a]	8.7	0.7	11.1	1.5	1.5	0.144

[a] Mean scores and standard errors were obtained by using the median height value for each assigned class and are presented only for comparative purposes. The statistic and associated *P*-value were derived using the Mann–Whitney *U*-test.

Table 5.4. Number of black bear den sites observed in Rocky Mountain National Park, Colorado per category of aspect and covertype from: 1) 1984–1991 (Historic) and 2003–2006 (Contemp) and 2) eastern and western sides of the continental divide from 1984–1991. Several similar covertypes were combined to facilitate estimation due to small sample sizes (mixed conifer with dead and down, aspen with mixed conifer with aspen, rock with herbaceous upland).

		Period				Location			
Variable	Class	Historic	Contemp	χ^2	*P*	East	West	χ^2	*P*
Aspect	North	11	9	7.1	0.069	9	2	9.8	0.020
	East	10	11			6	4		
	South	9	2			6	3		
	West	5	0			0	5		
Covertype	Lodgepole pine	9	5	11.7	0.040	3	6	4.7	0.195
	Mixed conifer	22	8			15	7		
	Rock	2	2			1	1		
	Douglas fir	2	1			2	0		
	Limber pine	0	4						
	Aspen	0	2						

Table 5.5. Maximum entropy models for each subset of parameters for both historic (1984–1991) and contemporary (cont; 2003–2006) black bear dens in Rocky Mountain National Park, Colorado. 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. Preferred models are in bold.

Study	Model[a]	AUC	SE	*Z*	*P*	Threshold	Class %
Historic	Slope, elev, covtype, droad, height, dtrail, aspect	0.913	0.015			24.688	77
	Slope, elev, covtype, droad, height, dtrail	0.905	0.013	1.249	0.212	25.682	77
	Slope, elev, covtype, droad, height	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	**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, height, covtype, elev, dtrail	0.937	0.016			23.146	86
	Slope, droad, aspect, height, covtype, elev	0.932	0.018	0.873	0.383	23.632	86
	Slope, droad, aspect, height, covtype	0.923	0.016	2.259	0.024	23.476	77
	Slope, droad, aspect, height	**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, height = canopy height, elev = elevation, droad = distance to nearest road, dtrail = distance to nearest trail.

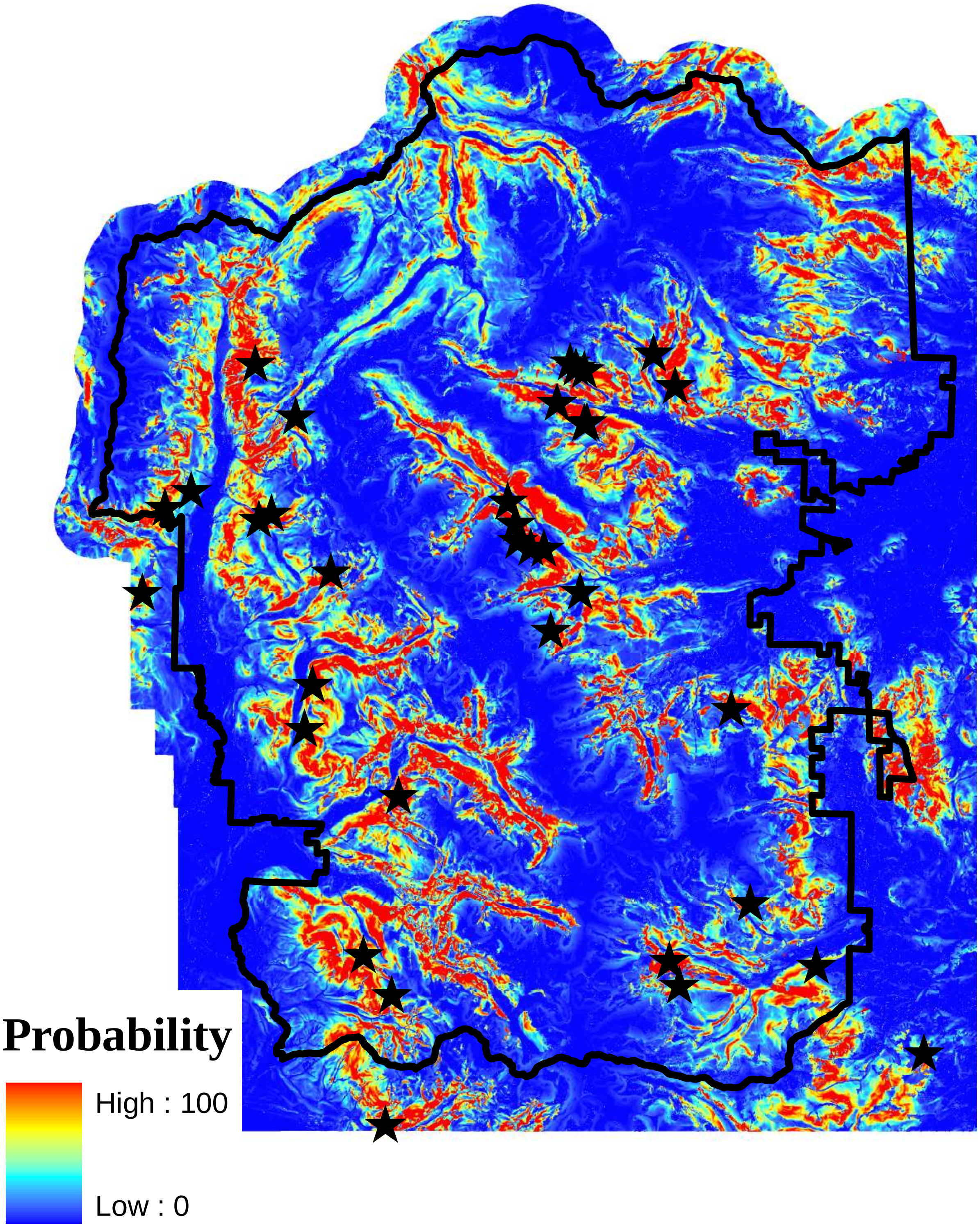

Figure 5.1. Map depicting the probability of denning locations for black bears in Rocky Mountain National Park, Colorado, 1984–1991. Black stars indicate observed den sites. Variables nested within the model include slope, elevation, and covertype. See text for description of variables.

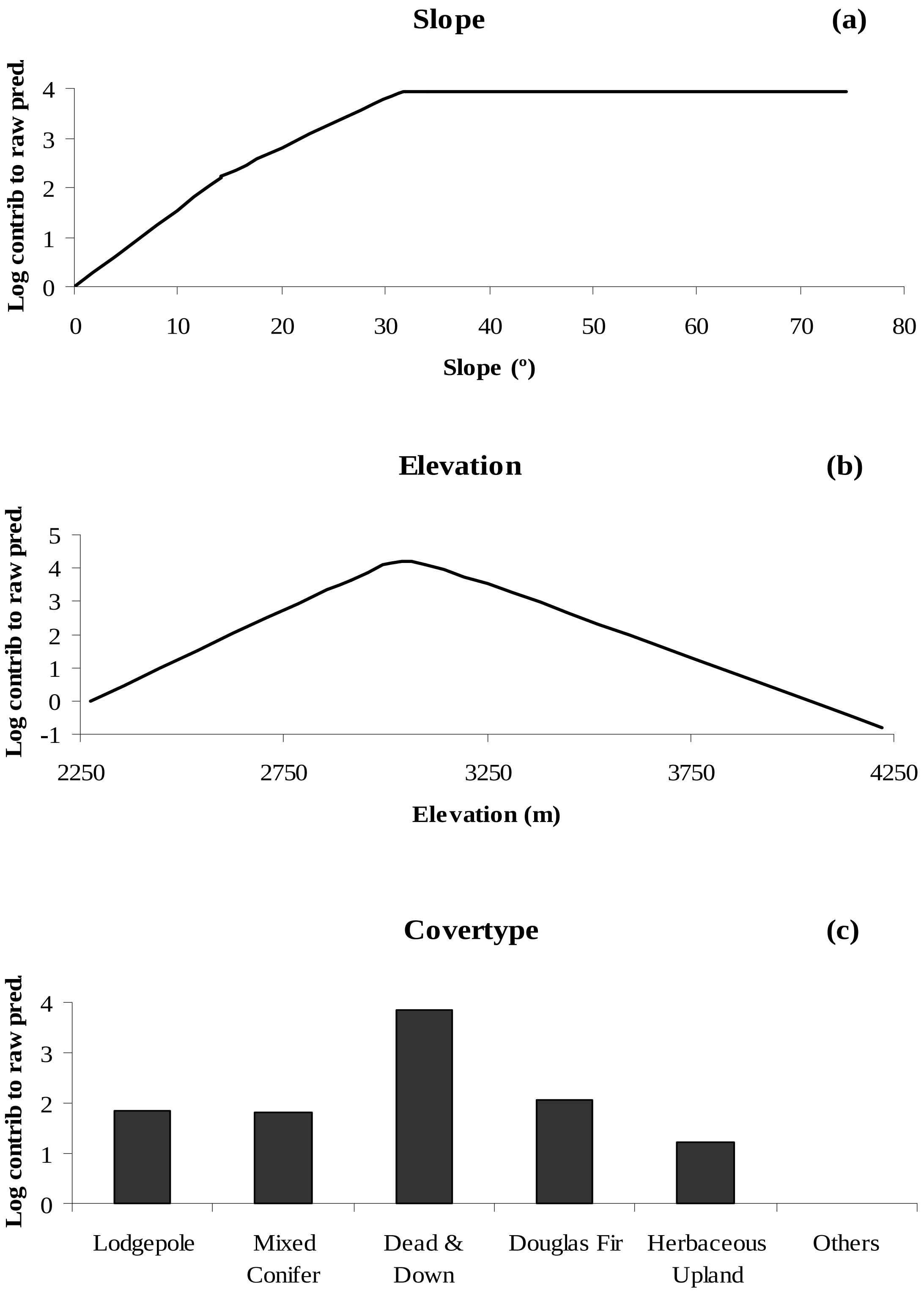

Figure 5.2. Relationships between the exponential contribution of slope (a), elevation (b), and covertype (c) to the raw prediction score and the observed value for 35 black bear den sites observed from 1984–1991 in Rocky Mountain National Park, Colorado.

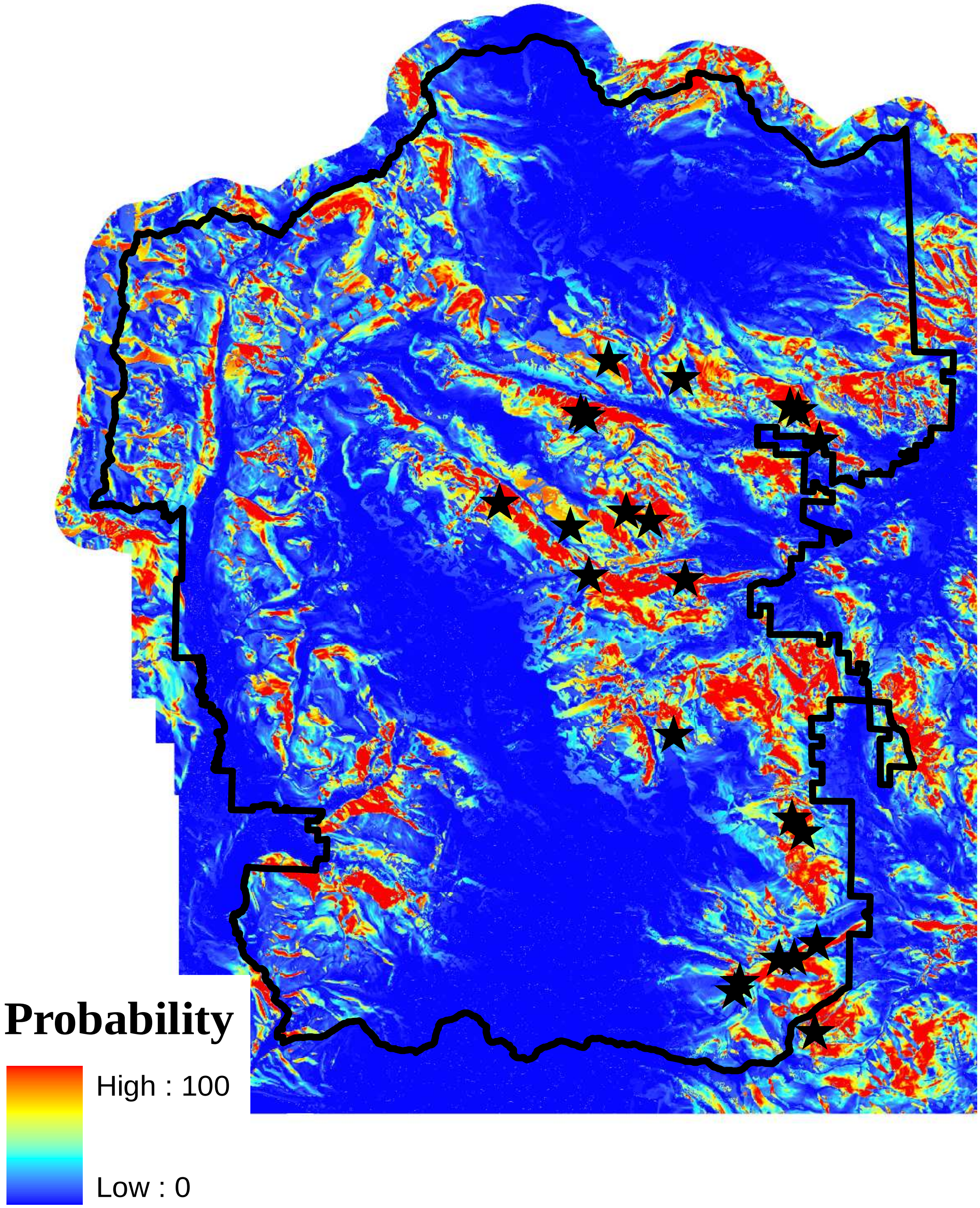

Figure 5.3. Map depicting the probability of black bear denning locations in Rocky Mountain National Park, Colorado, 2003–2006. Black stars indicate observed den sites. Variables nested within the model include slope, distance to roads, aspect, and canopy height. See text for description of variables.

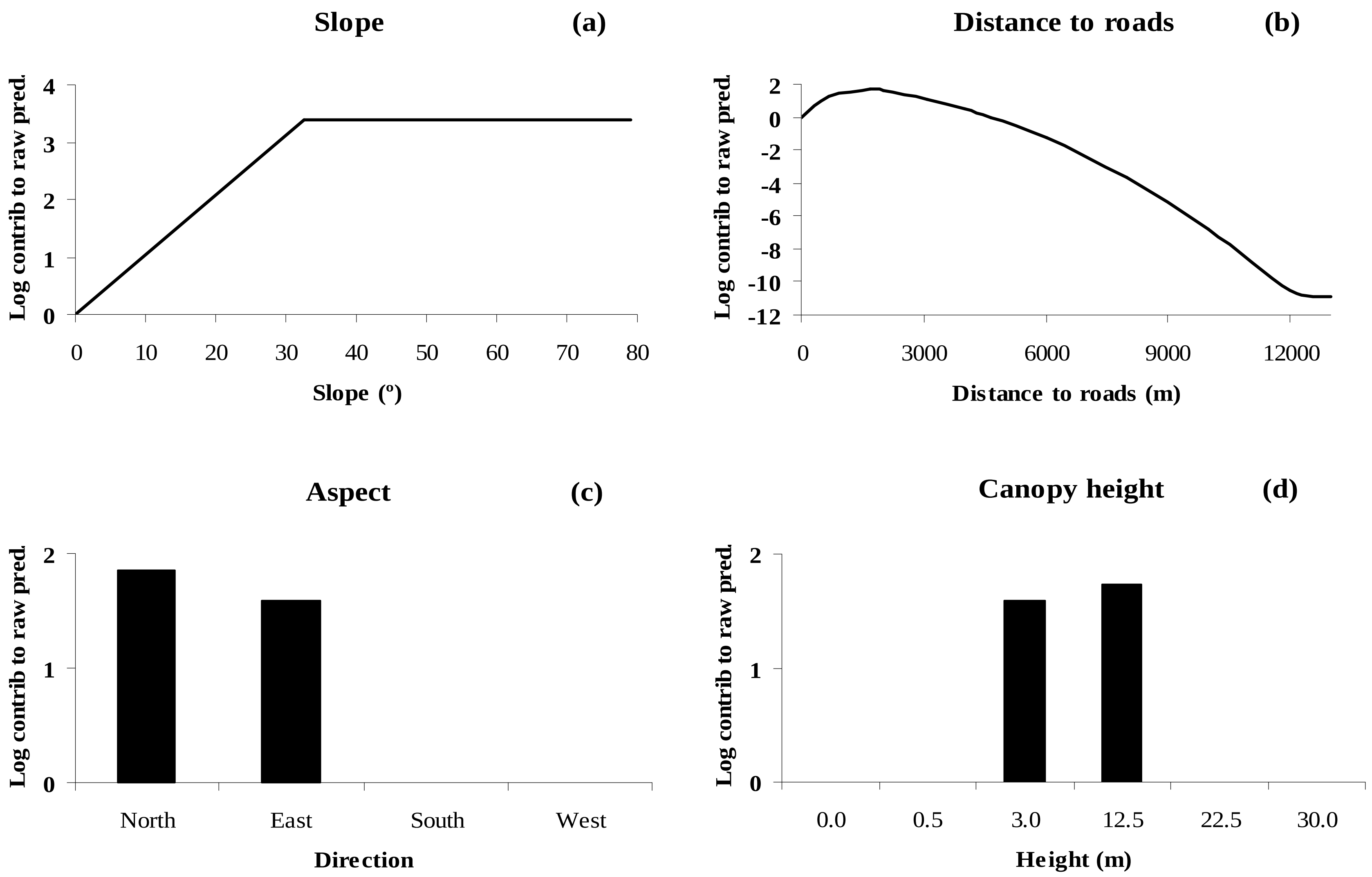

Figure 5.4. Relationships between the exponential contributions of slope (a), distance to roads (b), aspect (c), and canopy height (d) to the raw prediction score and the observed value for 22 black bear den sites observed from 2003–2006 in Rocky Mountain National Park, Colorado.

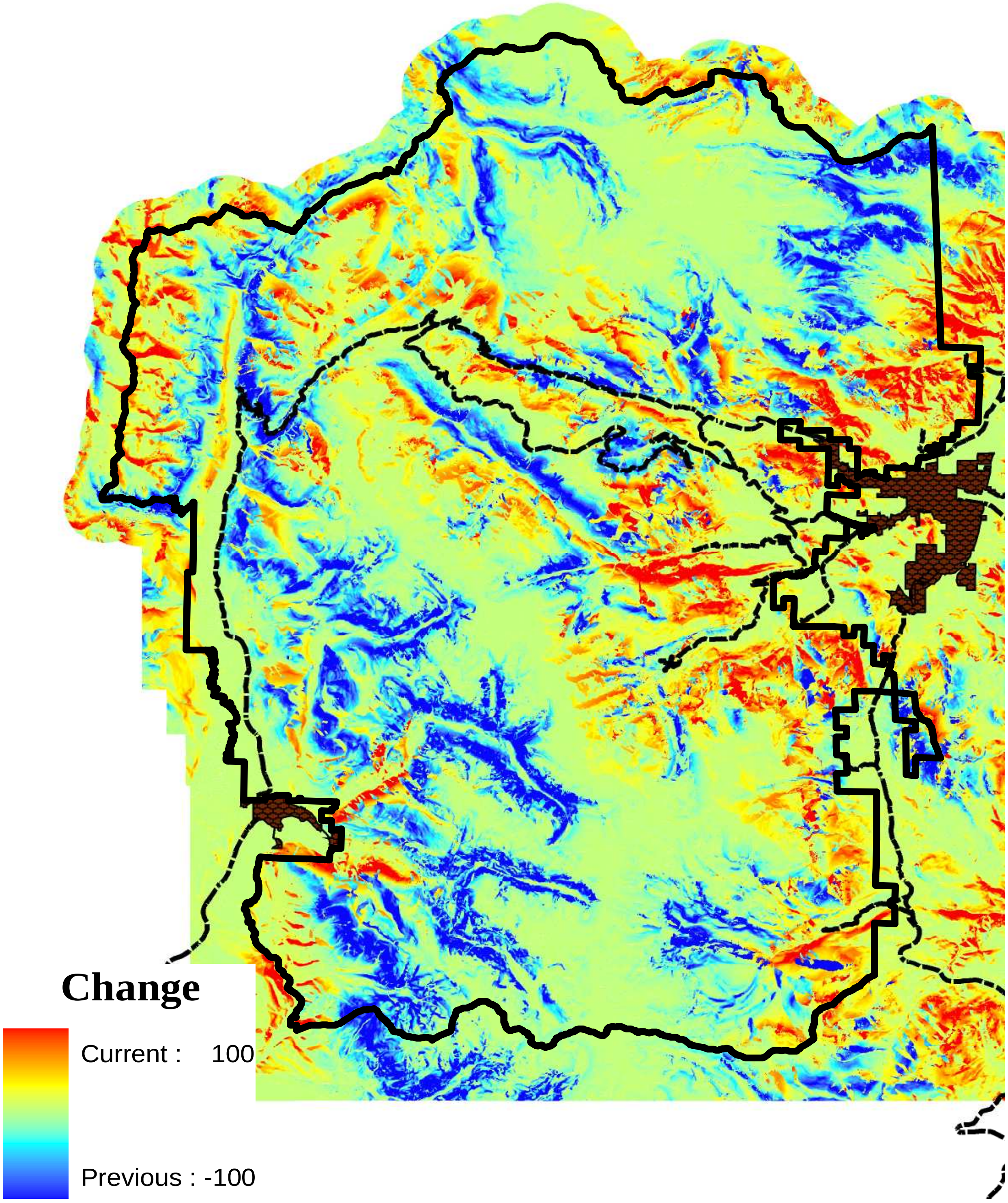

Figure 5.5. Map illustrating shift in predicted suitable black bear den locations from 1984–2006 in Rocky Mountain National Park, Colorado. Cooler colors represent sites historically suitable for denning but currently less utilized, while warmer colors illustrate areas currently selected for den sites but were previously less suitable. Roads are depicted by dashed lines, while brown cross-hatched areas represent urban sites.

Denning chronology

I recorded 22 (5 adult male, 1 subadult male, 10 adult female, 6 subadult female) denning occurrences from 2003–2006. Date of den entrance ranged from 12 October–27 November, while den exit varied from 30 March–12 May. The best model ($F_{2,17} = 17.6$, $P < 0.001$, $R^2 = 0.675$) for all denning occasions combined included age class and precipitation (Table 6) and indicated that subadult black bears denned earlier during drier years. This model excluded 2 outliers; these dates were from a large adult female in very good condition (2005 = 37% body fat, 2006 = 45% body fat; Chapter 2) which likely allowed her to den earlier (Rogers 1987). A model ($F_{2,15} = 14.6$, $P < 0.001$, $R^2 = 0.661$) including age class and temperature had similar explanatory power (Table 6). However, examination of residual plots for this model indicated 2 additional outliers.

Logistic analyses resulted in 4 competing models for denning period (early versus late; Table 7). The preferred models (Table 7) included age class (odds ratio = 66.3 [95% CI = 0.6–> 999.9]) and precipitation (odds ratio = 1.303 [95% CI = 1.004–1.691]) and age class (odds ratio = 27.6 [95% CI = 0.7–> 999.9]) and temperature (odds ratio = 0.039 [95% CI = 0.002–0.932]). Because CI's around odds ratios included 1 for age class, this variable was dropped as uninformative. These models indicated earlier denning in dry, warm years.

The best ($F_{1,6} = 57.0$, $P < 0.001$, $R^2 = 0.905$) linear regression model for the early denning period included only temperature (Table 6); warmer temperatures resulted in later den entrance. One outlier was observed; this female was the last to den in this group and was suspected to be pregnant (2 years since previous cub production with 39% body fat; R. Baldwin and L. Bender, unpublished data) thus potentially influencing date of den entrance (data collection ended before reproduction could be verified). Temperature was also the most

Table 5.6. Models relating time of den entrance and emergence of black bears to selected explanatory variables in Rocky Mountain National Park, Colorado, 2003–2006. Den entrance models were assessed for early (12 October–6 November) and late (16 November–27 November) denning periods and for both periods combined.

Behavior	Period	Model	*F*	*P*	R^2	*n*	Variable	*t*	*P*	β	SE
Entrance	Both	1	17.6	<0.001	0.675	20	Age class	–4.4	<0.001	–18.843	4.247
							Precipitation	4.2	<0.001	0.890	0.213
		2	14.6	<0.001	0.661	18	Age class	–2.9	0.011	–11.081	3.795
							Temperature	–4.6	<0.001	–11.581	2.499
Entrance	Early	1	57.0	<0.001	0.905	8	Temperature	7.5	<0.001	30.241	4.007
	Late	1	99.0	<0.001	0.917	11	Temperature	–10.0	<0.001	–6.346	0.638
Emergence		1	24.8	<0.001	0.692	13	Snowpack	–5.0	<0.001	–0.712	0.143
		2	23.8	<0.001	0.684	13	Precipitation	4.9	<0.001	11.073	2.270
		3	3.9	0.071	0.229	15	Sex	2.0	0.071	13.045	6.637

Table 5.7. Logistic regression models (ΔAIC's ≤ 4.0) and associated statistics relating early ($n = 9$) and late ($n = 13$) denning periods to selected explanatory variables for black bears in Rocky Mountain National Park, Colorado from 2003–2006.

		Variables				Model					
Model	Variable	χ^2	P	β	SE	χ^2	P	AIC	Δ AIC	R^2	% con
1	Age class	3.0	0.081	–4.195	2.407	13.1	0.001	22.63	0.00	0.606	83.8
	Precipitation	3.9	0.047	0.264	0.133						
2	Age class	3.0	0.082	–3.319	1.907	11.9	0.003	23.87	1.24	0.563	80.3
	Temperature	4.0	0.045	–3.246	1.620						
3	Sex	2.9	0.088	1.192	0.698	10.1	0.006	25.66	3.03	0.497	77.8
	Temperature	2.9	0.087	–3.295	1.927						
4	Sex	3.1	0.077	1.191	0.674	9.7	0.008	26.05	3.42	0.481	79.5
	Precipitation	3.0	0.081	0.208	0.119						

important variable in the best model ($F_{1,9} = 99.0$, $P < 0.001$, $R^2 = 0.917$) for the late denning period and indicated later denning during years with cooler temperatures (Table 6). Two outliers were removed from this group (adult male and adult female). Both denned later than expected with the female pregnant at the time of den entrance.

Den exit was related to both snowpack ($F_{1,11} = 24.8$, $P < 0.001$, $R^2 = 0.692$) and temperature ($F_{1,11} = 23.8$, $P < 0.001$, $R^2 = 0.684$) during March–April with greater snowpack and lower temperatures associated with earlier exit dates (Table 6). Although not as strong of a relationship, sex ($F_{1,13} = 3.9$, $P = 0.071$, $R^2 = 0.229$) was also associated with den exit as males emerged earlier from dens (Table 6). Construction of multivariate models did not strengthen these relationships.

DISCUSSION

Denning habitat

Maximum entropy efficiently modeled the 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. With the exception of slope, variables most closely associated with den sites differed between historical and contemporary den sites (Tables 2 and 3). 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). Steep slopes were consistently important for the selection of den sites regardless of the sample period, peaking at 31º–32º, and slopes from RMNP den sites fell well within the 20º–40º range reported by others (Beecham et al. 1983, LeCount 1983, Mack 1990, Hayes and Pelton 1994, Costello et al. 2001).

Historically, elevation and covertype were also important in den-site selection. Black 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). Also, den sites at 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. Interestingly, 1 non-forested covertype (herbaceous upland) was also selected for. Use of such sites have been noted elsewhere (i.e., west-central Colorado, Beck 1991) but were not likely preferred.

In addition to steeper slopes, contemporary black bear dens were associated with north and east facing aspects, mid-level canopies, and sites closer to roads (Tables 2 and 3). Preferred aspects of dens appear to vary with location (Novick et al. 1981, LeCount 1983, Mack 1990, Hayes and Pelton 1994, Costello et al. 2001), although northern aspects are often used given their greater levels of shading and subsequent snow cover. Selection of eastern aspects in RMNP may have been influenced by their greater availability given the absence of den sites west of the continental divide. Although canopy heights of 2–15 m had a greater influence on the probability of den occurrence than other heights, I noticed that the majority of the 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). Interestingly, contemporary den sites were closer to roads, which was unusual as black bears typically den away from human-use areas (Goodrich and Berger 1994, Linnell et al. 2000, Gaines 2003). Such proximity to heavy-use areas may indicate habituation to humans (Beckmann and Berger 2003a), and greater use of human-influenced habitats (see Chapter 7).

The change in factors included in preferred models between the 2 sampling periods was likely due to a shift in denning preferences by black bears over the last 15–20 years. I found contemporary dens at consistently lower elevations and closer to roads and trails than previously observed. These shifts were likely related to movements from more remote, higher elevation locations to sites closer to heavy human-use areas. Earlier work suggested that RMNP's black bear population exhibited cryptic behavior (McCutchen 1990) and selected den sites away from human-use areas (Zeigenfuss 2001). However, the presence of human-use areas no longer appears to prohibit denning of all black bears in RMNP. In fact, I observed 2 black 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, presumably a learned response to the increase in anthropogenic food sources present at the urban-wildland interface (Beckmann and Berger 2003a, b). This shift in core-use areas and associated food sources led to an increase in overall body weight and condition in Nevada. I observed comparable results for females in RMNP during summer, as weights, percent body fat, and body condition index of females increased from historic to contemporary periods (see Chapter 2), suggesting a similar response in use patterns and associated conditioning to humans (see also Chapters 6 and 7). Black bear dens were not associated with any particular covertype in the contemporary period. The reason for this change is unclear, although a gradual shift towards heavy human-use areas, presumably because of greater availability of and benefits associated with anthropogenic foods (see Chapter 7), may have been more important to denning than any particular cover type. Presence of autumn food sources has been suggested to influence den-site selection in other areas (i.e., southern California, Novick et al. 1981).

Although aspect differed between periods, this was likely an artifact of the inclusion of west-side localities in historic den sites. Additionally, even though slope and canopy height did not differ between sample periods, both were important in predicting den distribution in the contemporary period. Steep slopes appear to be a requisite for suitable den sites in RMNP regardless of proximity to human-use areas. Additionally, the same canopy heights were preferred during both periods though this variable was not included in the preferred model for historical den sites as a more parsimonious model provided equal fit.

Denning chronology

As observed in other studies (e.g., Graber 1990, Smith et al. 1994), the relationship between ecological and environmental variables and den entrance was highly variable. Sex was not significant in den-entrance models for RMNP, although male black bears often den later than females (LeCount 1980, O'Pezio et al. 1983, Beck 1991, Smith et al. 1994). This may have been due to few observed denning occasions by males, as males exhibited later den entrance dates than females in RMNP (males: $\bar{x}$ = day 321, SE = 5, n = 6; females: $\bar{x}$ = day 312, SE = 4, n = 16). Similar to other results in Colorado, elevation also was not related to den entrance (Beck 1991). Snowfall impacted den entrance dates in some areas (e.g., Jonkel and Cowan 1971), though most found it to be inconsequential (Beecham et al. 1983, O'Pezio et al. 1983, Beck 1991, Schooley et al. 1994, Smith et al. 1994). Unfortunately, snowfall data was insufficient for analysis in this study, although I do not believe it influenced denning as little snowfall was present when many black bears denned, while others maintained activity with 15–30 cm present.

In contrast to other studies (e.g., Kolenosky and Strathearn 1987, Smith et al. 1994), I observed earlier denning by subadults. Subadult females in my population were in poorer condition than adults during early hibernation (adult body fat = 38%, subadult body fat = 24%; see Chapter 2); typically black bears in poor condition den later than those in good condition (Rausch 1961, Carpenter 1973, Hamilton and Marchinton 1980). However, dominant black bears can act as despots by excluding others from preferred foraging locations resulting in later den entrance for dominant individuals (Beckmann and Berger 2003b). Many adult black bears in RMNP readily consumed anthropogenic foods (see Chapter 6), leading to high condition levels (see Chapters 2 and 7). The exclusion of subadults from high quality food patches (typically anthropogenic food sources) may explain the disparity in date of den entrance.

Body condition and food availability were likely the ultimate factors influencing date of den entrance in RMNP (Johnson and Pelton 1980, Beecham et al. 1983, Schooley et al. 1994, Costello et al. 2001). My use of precipitation and maximum temperature as surrogates for vegetative productivity and condition yielded mixed results. Models predicted later den entrance during years with greater precipitation and lower temperatures, suggesting that greater forage productivity led to later denning dates. In support of this, I observed that the only 2 subadults that denned in the late period did so during the wettest, coolest year. However, a different trend with temperature was observed between the early and late denning periods. Black bears denned in the late denning period during wet years, and later within this period if the year was particularly cool. Conversely, black bears denned in the early denning period during drier years, but denned later within this period if that year was warmer. This suggested a threshold level response to environmental cues as precipitation and temperature influenced both the period when they denned and the time-frame within this period when they denned and further supports the complex nature of predicting the onset of denning.

Models predicting den exit appear counterintuitive and are difficult to explain, as I observed earlier den exits during colder years with greater snowpack. Typically, black bears exit dens earlier during warmer years, as warm weather melts the snow and can cause flooding of dens (Alt 1984, Kolenosky and Strathearn 1987, Rogers 1987). Leaving dens earlier during cold years with abundant snowpack would likely not benefit black bears. Therefore, I suggest little influence of snowpack and temperature on den exit which supports a similar finding in west-central Colorado (Beck 1991). However, the influence of sex on den emergence was expected as males typically emerge earlier than females (Kolenosky and Strathearn 1987, Smith et al. 1994, Gaines 2003). Although I did not observe a strong relationship with sex, this was once again likely influenced by the small number of males sampled.

MANAGEMENT IMPLICATIONS

Preferred denning locations of black bears shifted between historic and contemporary periods in RMNP, indicating that critical habitat features of species can change over time. Managers thus should periodically review prescriptions for meeting critical life requisites of species to ensure that they are still relevant. Increased use of denning sites close to relatively high human-use areas suggests that black bears have become increasingly tolerant or habituated to humans in RMNP, increasing the amount of potentially suitable denning habitat and thus decreasing the likelihood that suitable den sites are limited in RMNP.

LITERATURE CITED

Alt, G. L. 1984. Black bear cub mortality due to flooding of natal dens. Journal of Wildlife Management 48:1432–1434.

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.

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

Beckmann, J. P., and J. Berger. 2003a. 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. 2003b. 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.

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.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.

Carpenter, M. 1973. The black bear in Virginia. Virginia Commission of Game and Inland Fisheries, Richmond, Virginia, USA.

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, New Mexico, USA.

DeGayner, E. J., M. G. Kramer, J. G. Doerr, and M. J. Robertsen. 2005. Windstorm disturbance effects on forest structure and black bear dens in southeast Alaska. Ecological Applications 15:1306–1316.

Eberhardt, L. L. 2003. What should we do about hypothesis testing? Journal of Wildlife Management 67:241–247.

Elowe, K. D. 1984. Home range, movements, and habitat preferences of black bear (*Ursus americanus*) in western Massachusetts. Thesis, University of Massachusetts, Amherst, Massachusetts, 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.

Graber, D. M. 1990. Winter behavior of black bears in the Sierra Nevada, California. International Conference on Bear Research and Management 8:269–272.

Hamilton, R. J., and R. L. Marchinton. 1980. Denning and related activities of black bears in the coastal plain of North Carolina. International Conference of Bear Research and Management 4:121–126.

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.

Hayes, S. G., and M. R. Pelton. 1994. Habitat characteristics of female black bear dens in northwestern Arkansas. International Conference on Bear Research and Management 9:411–418.

Hosmer, D. W., and S. Lemeshow. 2000. Applied logistic regression. Second edition. John Wiley & Sons, New York, New York, USA.

Johnson, K. G., and M. R. Pelton. 1980. Environmental relationships and the denning period of black bears in Tennessee. Journal of Mammalogy 61:653–660.

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.

Jonkel, C. J., and I. McT. Cowan. 1971. The black bear in the spruce-fir forest. Wildlife Monographs 27.

Koehler, G. M., and D. J. Pierce. 2003. Black bear home-range sizes in Washington: climatic, vegetative, and social influences. Journal of Mammalogy 84:81–91.

Kolenosky, G. B., and S. M. Strathearn. 1987. Winter denning of black bears in east-central Ontario. International Conference on Bear Research and Management 7:305–316.

LeCount, A. L. 1980. Some aspects of black bear ecology in the Arizona chaparral. International Conference on Bear Research and Management 4:175–179.

LeCount, A. L. 1983. Denning ecology of black bears in central Arizona. International Conference on Bear Research and Management 5:71–78.

Lindzey, F. G., and E. C. Meslow. 1976. Winter dormancy in black bears in southwestern Washington. Journal of Wildlife Management 40:408–415.

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. K., 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.

Nagelkerke, N. J. D. 1991. A note on a general definition of the coefficient of determination. Biometrika 78:691–692.

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.

O'Pezio, J., S. H. Clarke, and C. Hackford. 1983. Chronology of black bear denning in the Catskill region of New York. International Conference on Bear Research and Management 5:87–94.

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., M. Dudík, and R. E. Schapire. 2004. A maximum entropy approach to species distribution modeling. Pages 655–662 *in* Proceedings of the 21st International Conference on Machine Learning, ACM Press, New York, New York, USA.

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

Ramsey, F. L., and D. W. Schafer. 1997. The statistical sleuth: a course in methods of data analysis. Duxbury Press, Belmont, California, USA.

Rausch, R. L. 1961. Notes on the black bear (*Ursus americanus* Pallus) in Alaska with particular reference to dentition and growth. Zeitschrift fur Sangetierkunk 26:77–107.

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.

Schoen, J. W., L. R. Beier, J. W. Lentfer, and L. J. Johnson. Denning ecology of brown bears on Admiralty and Chichagof islands. International Conference on Bear Research and Management 7:293–304.

Schooley, R. L., C. R. McLaughlin, G. J. Matula, Jr. and W. B. Krohn. 1994. Denning chronology of female black bears: effects of food, weather, and reproduction. Journal of Mammalogy 75:466–477.

Schwartz, C. C., S. D. Miller, and A. W. Franzmann. 1987. Denning ecology of three black bear populations in Alaska. International Conference on Bear Research and Management 7:281–291.

Smith, M. E., J. L. Hechtel, and E. H. Follmann. 1994. Black bear denning ecology in interior Alaska. International Conference on Bear Research and Management 9:513–522.

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.

Zeigenfuss, L. C. 2001. Ecology of black bears in Rocky Mountain National Park: an analysis of population dynamics, diet, and habitat selection (1985–1991). Unpublished report, U.S. National Park Service, Rocky Mountain National Park, Colorado, USA.

Chapter 6:

Food habits and nutritional components of black bears in Rocky Mountain National Park, Colorado

Roger A. Baldwin, Department of Animal and Range Sciences, New Mexico State University, P.O. Box 30003 MSC 4901, Las Cruces, New Mexico 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, New Mexico 88003, USA

Chapter summary: Knowing food items utilized by local black bear populations is a necessary step towards implementing effective management strategies or identifying critical habitats, as available food items vary geographically and among habitat types. Knowing the nutritional composition of selected foods also aids this understanding by identifying food sources most beneficial to the population. Therefore, we collected black bear (*Ursus americanus*) scats from 2003–2006 to determine important foods and relative nutritional values of those foods for black bears in Rocky Mountain National Park (RMNP), Colorado. To determine dietary composition, we conducted volumetric analyses on collected scats. We then adjusted volumetric values using conversion factors to better estimate the consumed volume of each food item, and tested subsamples of each scat for gross energy (cals/gm), crude fat (%), and fecal nitrogen (%). We compared the converted volumetric values and nutritional components to determine important sources of energy, fat, and protein. We also conducted focal animal observation on radiocollared black bears to corroborate dietary composition values derived from scat analyses. All analyses were conducted annually and seasonally. Lastly we compared the percentage of scats containing anthropogenic food sources from historic (1984–1991) and contemporary (2003–2006) periods in RMNP to determine if black bears have increased use of such food sources over the last 15–20 years. Adjusted volumetric values were highest annually for grasses (24.2%), berries (16.8%), and ants (31.2%). Use of grasses ($H_2 = 21.8$, $P < 0.001$), berries ($H_2 = 10.1$, $P = 0.007$), and small mammals ($H_2 = 5.4$, $P = 0.068$) varied by season, with greatest use of grasses (49.1%) occurring during spring and berries (31.6%) and small mammals (14%) during autumn. Focal animal observation yielded similar trends annually for time spent foraging on grasses (17.8), berries (10.2), and insects (61.3) with all 3 differing between spring and summer seasons (grass: $U = 253.0$, $P < 0.001$; berries: $U = 84.5$, $P = 0.009$; insects: $U = 91.0$, $P = 0.076$); no analyses were conducted for autumn given small sample sizes. Nutritional assessments indicated highest values for gross energy ($H_2 = 9.7$, $P = 0.008$) and crude fat ($H_2 = 4.9$, $P = 0.085$) during summer; no seasonal differences were noted for fecal nitrogen ($H_2 = 4.3$, $P = 0.119$). Gross energy was typically lowest for grasses and other herbaceous plants and highest for ants and ungulates. Fecal nitrogen was strongly related to most animal sources but was negatively correlated with vegetative matter. Crude fat showed the strongest positive relationship with berries, though this was likely influenced by the presence of seeds in the analysis. Collectively, fecal remains appeared to be less effective in interpreting crude fat of black bear diets than for gross energy or fecal nitrogen. Greater frequency of ants (Fisher's exact $P < 0.001$) but less grass (Fisher's exact $P < 0.001$) was observed in historic black bear diets, while contemporary diets included substantially greater amounts of anthropogenic foods (Fisher's exact $P < 0.0001$). This increased use of human foods likely contributed to increases in observed body size (weight females: historic = 52 kg, contemporary = 58 kg), body condition (body fat females: historic = 15.0%, contemporary = 22.8%), and population growth rate (historic $\lambda = 1.01$, contemporary $\lambda = 1.11$) for the contemporary black bear population.

Black bear (*Ursus americanus*) diets vary geographically depending on food sources available to bears. For example, in deciduous forests of the eastern U.S., black bears heavily utilize hard and soft mast crops (Pelton 2003), while ants are heavily used in north-central Minnesota (Noyce et al. 1997). Knowledge of food sources utilized by local black bear populations should provide insight into reproductive rates, condition, and habitat selection of black bears, thus allowing effective management of these populations (McDonald and Fuller 1994). One of the most commonly used techniques for assessing food habits is scat analysis.

Most commonly, food items are identified and related to diets through frequency, relative density, or volume (e.g., Raine and Kansas 1990, Hellgren 1993, Kasbohm et al. 1995). However, these approaches do not account for the differing digestibilities of food items. Therefore, correction factors were developed for common food items to account for these differing digestibilities (Hewitt and Robbins 1996), with the use of corrected volumetric values allowing for more accurate identification of important food items. Focal animal observation provides an alternative method for assessing food habits. This method relies on the ability of the observer to follow an individual for a select period of time while recording activities of the subject (Morrison et al. 1992, MacDonald et al. 2000). This technique allows for direct knowledge of foods each animal consumes and provides a corroborative technique for estimating black bear dietary habits.

However, identification of food sources consumed does not necessarily indicate which food items are most beneficial to black bears, whereas knowledge of nutritional composition of food items does provide insight into which food sources supply the greatest amount of energy and other nutrients for black bears (Gluesing and Field 1986). Several investigations have attempted to delineate this relationship (e.g., Elowe and Dodge 1989, Kasbohm et al. 1995) by relating nutritional components of selected foods to quantities consumed. However, nutritional composition of the same species can vary substantially from plant to plant and even within the same plant (Holechek et al. 2004). Alternatively, nutritional components of fecal material from species with ruminant and monogastric stomachs have been used to assess dietary quality (Leslie and Starkey 1985, Hodgman et al. 1996, Magomedov et al. 1996). Assessing nutritional components from black bear scats could provide similar information and has the added advantage of directly representing the nutritional composition of foods consumed rather than estimating values for food sources that might not be representative of those consumed by bears. Nonetheless, food sources have a variety of digestibilities with respect to nutritional components (Pritchard and Robbins 1990). Therefore, estimates derived from consumed foods (i.e., scats and stomach content) may simply represent relative levels of nutritional components rather than direct values, but still likely reflect quality of diets consumed (Magomedov et al. 1996, Clark et al. 2003).

Nutritional components that are important to black bears include gross energy, fat, and protein (represented in analyses by fecal nitrogen). Consumption of energy-rich foods is an important consideration for black bears given their need to accrue large stores of fat for hibernation (Pelton 2003). High energy foods include most soft mast producing plants (i.e., *Vaccinium* spp, *Ribes* spp., *Rubus* spp.) as well as fat and protein-rich food sources such as hard mast, insects, and ungulates (Swenson et al. 1999, Rode and Robbins 2000, Inman and Pelton 2002). Additionally, high protein diets result in increased weight gains and fecundity in black bears, indicating the importance of such foods in bear diets (Tate and Pelton 1983, Rogers 1987, McLean and Pelton 1990, Beckmann and Berger 2003a). Therefore, foods high in 1 or more of these components are more important for black bears because of the direct relationship to increased individual condition and hence individual and population performance.

Consumption of human foods can also be an important consideration in many areas, as these foods are generally high in fat and protein (components of black bear diets that are generally lacking) and are easily obtained (Pelton 2003). Unfortunately, the utilization of human foods often brings black bears into direct contact with humans and can ultimately lead to conflicts (Zardus and Parsons 1980, Herrero 2002, Beckmann and Berger 2003b). For example, Tate and Pelton (1983) reported 624 aggressive actions by panhandling black bears in Great Smoky Mountain National Park, with 6% of these aggressive acts leading to actual physical contact with humans. In the Sierra Nevada-Great Basin interface, Beckmann and Berger (2003b) found that increased abundance of human foods led to a rapid shift of wildland black bears to urban areas, a heavily skewed sex ratio towards males, changes in female reproductive success, an increase in body mass, and a reduction in home-range size, time spent foraging, and time spent in dens. Understanding the level of use of anthropogenic food sources by black bears can help identify potential problem situations and allow for appropriate management actions to alleviate this situation.

Historically, food habits assessed for black bears in Rocky Mountain National Park (RMNP), Colorado, from 1984–1991 indicated heavy use of animal matter compared to other localities (47.7% of scats; Zeigenfuss 2001), although direct comparisons with other studies is difficult because food habits were not assessed volumetrically precluding the application of correction factors to more accurately represent foods consumed. RMNP’s black bear population is unique in that it is one of the highest elevation populations of black bears in the U.S. Such high elevations result in a substantially shorter growing season and a lack of hard mast crops often utilized by black bears in other localities. These factors were believed to be the cause of the small size of black bears (adult male = 80 kg, adult female = 55 kg; Zeigenfuss 2001) reported in RMNP historically. However, recent observations (2003–2006, hereafter contemporary) suggest increased size (adult male = 99 kg, adult female = 68 kg; Chapter 2) and condition (body fat females: historic = 15.0%, contemporary = 22.8%; Chapter 2) over historic (1984–1991) populations, a result most parsimoniously related to changes in foods consumed by black bears in RMNP. Therefore, I collected scats and observational data from 2003–2006 to assess contemporary food habits of black bears in RMNP, and compared frequency of occurrence of food items between historic and contemporary periods to assess shifts in use of food sources over time. I also analyzed scats for gross energy, crude fat, and fecal nitrogen to determine food sources most strongly related to these nutritional components. I conducted analyses annually and seasonally to determine seasonal trends in food habits and nutritional components. Lastly, I compared the use of anthropogenic foods between historic and contemporary periods to assess potential differences in use between these time periods.

METHODS

Food habits

I collected black bear scats when encountered during associated field activities (i.e., bear capture, telemetry, focal animal observations, and vegetation surveys; Baldwin 2008) from summer 2003–autumn 2006 with location, date collected, and approximate age (< 1 week, 1–4 weeks, > 4 weeks) recorded for each scat. For analysis, I soaked each fecal sample in water and antibacterial soap overnight. I then rinsed samples in hot and cold water for 5 minutes over 2.38-mm and 1-mm soil-screens. I spread remaining materials on a tray and mixed them thoroughly with 10–33% of the remaining food items randomly selected for further analysis (Hewitt and Robbins 1996). I then submerged these materials in water to allow easier separation of food items. Scat items were placed into 1 of 10 categories including grasses, other herbaceous plants (hereafter, herbaceous), berries, hard mast, ants, other insects (hereafter, insects), small mammals, ungulates, garbage, and non-food items (see Table 1 for further description). I identified plant materials using reference collections and plant identification keys (i.e., Feucht 1999, Beidleman et al. 2000), while small mammals and ungulates were identified from hair and bone remains using reference collections and hair keys (Moore et al. 1974). Once I completed identification, I squeezed excess water from food items and estimated volume using water displacement in a graduated cylinder (Hewitt and Robbins 1996).

I applied correction factors (grass = 0.26, herbaceous = 0.26, berries = 0.93, hard mast = 1.5, ants = 1.74, insects = 1.1, small mammals = 4.0, neonate ungulates = 1.5, other ungulates = 3.0) to volumetric estimates of food items to account for differing digestibilities of food items (Hewitt and Robbins 1996, Bunnell 2000). No correction factors were available for garbage items (i.e., plastic, paper, rubber, aluminum foil). Therefore, I excluded scats containing these items from analyses involving correction factors given that even for food items in which I had established correction factors, corrected volumes might be inaccurate given the unknown volume of anthropogenic foods consumed. When I collected multiple scats known to have been deposited from the same individual from a single feeding bout, I averaged these samples with the mean serving as a single observation.

Table 6.1. Description of dietary classes used to categorize diets of black bears in Rocky Mountain National Park, Colorado, 2003–2006.

Scat items	Description
Grass	All monocots including grasses, sedges, and rushes.
Herbaceous	All forbs and leafy plant material but primarily *Vaccinium* spp., *Taraxacum* spp., and *Heracleum sphondylium*.
Berries	All berries but primarily *Vaccinium* spp., *Ribes* spp., *Sheperdia canadensis, Arctostaphylos uva-ursi*, and *Prunus virginiana*.
Hard mast	Sunflower seeds from bird feeders.
Ants	All ant species.
Insects	All insects other than ants but primarily wasps.
Small mammals	Members of Rodentia and Lagomorpha.
Ungulates	*Odocoileus hemionus* and *Cervus elaphus*.
Garbage	Includes primarily plastic, paper, rubber, and aluminum foil.
Non-foods	Primarily woody debris, soil, and sand.

I determined seasonal dietary composition of black bear diets by placing collected scats into spring (May–June), summer (July–August), and autumn (September–November) categories. I used the median date between date of collection and last day of approximate age (either 1 or 4 wks) for scats where date of deposit was unknown. I did not use any scats in seasonal analyses that were aged > 4 weeks given high uncertainty about the date of deposit. I compared diets across seasons and among years for both uncorrected and corrected volumetric percentages using Kruskal–Wallis tests (Zar 1999).

I also compared the frequency of primary food items per scat (i.e., food item with the greatest percent occurrence in each scat; Rosas-Rosas et al. 2003) between the historic and contemporary periods (χ^2 test; Zar 1999) to assess shifts in dietary constituents across time; I was not able to compare volumetric measures given the lack of such data for the historic period. Food items were classed as grass, herbaceous, berry, insect, and animal materials; I could not further define insect (i.e., ants and other insects) and animal (i.e., ungulates and small mammals) classes given the lack of specificity for these food items from historic scats. If I observed a significant difference ($\alpha = 0.05$) between historic and contemporary black bear populations, I used Fisher's exact test with a Bonferroni correction ($\alpha = 0.01$) for multiple comparisons to compare food items between time periods (Zar 1999). Unfortunately, I could not compare scats seasonally, as collection dates were not recorded historically. Therefore, results represent an exploratory comparison between historic and contemporary diets in RMNP. I also compared the number of scats with anthropogenic food sources to the total number of scats sampled using Fisher's exact test (Zar 1999) for both the historic and contemporary periods in RMNP to assess differences in utilization of these food sources. This analysis was conducted separately from the other frequency comparisons given a larger available data set including presence of anthropogenic foods for the historic period.

Observational analysis

I used modified Aldrich foot snares and culvert traps to capture black bears from 2003–2006. I immobilized bears with a 5:1 mixture of ketamine hydrochloride and xylazine hydrochloride (200 mg ketamine and 40 mg xylazine per ml) and fit bears with radiocollars. I radiotracked collared individuals from May through the time of den entrance and collected observational data on foraging behavior when I was able to get within visual range without alerting the bear to my presence. I noted observations every minute until the bear moved off or became alerted to my presence, and only foraging bouts with at least 10 minutes of observation were included in analyses. I classed foraging events as foraging on grasses, other herbaceous plants, berries, insects, and anthropogenic sources. Because I never observed foraging for vertebrates, this category was excluded from observational analyses. I used Mann–Whitney *U*-tests (Zar 1999) to compare differences between spring and summer seasons. Autumn was not used in seasonal analyses given a limited sample size for this season (n = 4).

Nutritional analysis

Before soaking scats, I manually mixed and collected a sub-sample from each scat for use in nutritional analyses for gross energy (GE; cals/gm), crude fat (FAT; %), and fecal nitrogen (FN; %). I determined GE using a bomb calorimeter (IKA C5000 model), FN by a carbon/nitrogen analyzer (Leco Truspec model), and FAT by ether extract using a Goldfisch (Labconco) apparatus. In addition, I determined total ash for each sample to convert nutritional components from dry matter to an organic matter basis. All chemical nutritional analyses were conducted by The Wildlife Habitat Nutrition Laboratory, Pullman, Washington, USA. In addition to calculating annual means for nutritional components, I also compared seasonal values using procedures defined previously for food composition analyses.

I used simple and multiple linear regression (Zar 1999) to relate corrected volumetric percentages of food items in scats to GE, FAT, and FN. I assessed outliers using residual plots (Zar 1999). Additionally, I used Spearman rank correlations to assess collinearity among variables; if variables were correlated at $r_s \geq 0.70$, only the more influential variable was included in further analyses to reduce redundancy (Agresti 1996) unless correlated variables had no functional relationship to each other. I compared resultant models using Akaike's information criterion (AIC; Burnham and Anderson 1998), and considered only models with ΔAIC's < 4 as competing models (Burnham and Anderson 1998). I also used R^2 values to aid model selection (Zar 1999), particularly for single variable models. I conducted these analyses annually and seasonally to assess the seasonal influence of food items on nutritional components. Scats containing hard mast were not included in regression analyses as all hard mast was from anthropogenic sources, hard mast was observed in only 5 of 128 scats for which I had nutritional data, and because most of these scats were extreme outliers.

RESULTS

Grasses, berries, and ants comprised the largest percentage of black bear diets in RMNP based on uncorrected fecal volume analyses (Table 2). Collectively, vegetative material made up 57.3% of annual black bear diets, animal matter comprised 28.9%, while garbage (5.2%) and non-food items (8.2%) accounted for the rest. Seasonally, fecal volume for grasses ($H_2 = 20.2$, $P < 0.001$), ants ($H_2 = 5.3$, $P = 0.072$), and berries ($H_2 = 16.8$, $P < 0.001$) varied, whereas all other foods were similar ($H_2 \geq 3.3$, $P \geq 0.195$). Use of grasses declined seasonally, use of berries

Table 6.2. Percentage volume of items observed in fecal samples (Uncorrected), as well as corrected values indicating percentage of diet composition of ingested foods (Corrected) for black bears in Rocky Mountain National Park, Colorado from 2003–2006. Correction factors are listed in text, although none were available for garbage and non-food items. Therefore, corrected percentages are listed for food-items only. Annual values included all scats observed, while seasonal values included only scats estimated at < 4 weeks old to reduce the potential for assigning scats to incorrect seasons.

	Percentage Fecal Volume Uncorrected[a]						Percentage Fecal Volume Corrected[b]					
	Annual	Spring	Summer	Autumn	*H*	*P*	Annual	Spring	Summer	Autumn	*H*	*P*
Grass	27.7	53.0A[c]	22.5B	3.1C	20.2	<0.001	24.2	49.1A	17.5B	0.7C	21.8	<0.001
Herbaceous	11.2	9.8	12.5	10.3	0.9	0.629	7.2	8.4	5.9	7.6	0.1	0.959
Berries	16.1	5.3A	17.2B	36.0C	16.8	<0.001	16.8	5.8A	20.5B	31.6B	10.1	0.007
Hard mast	2.3	0.2	2.0	6.8	1.0	0.599	2.8	0.4	1.9	10.3	2.9	0.229
Ants	15.7	7.5A	23.9B	11.2A	5.3	0.072	31.2	21.6	40.3	24.7	2.0	0.376
Insects	3.2	1.5	4.3	3.5	3.3	0.195	6.1	3.7	6.6	11.1	2.5	0.281
Small mammals	3.9	3.7	2.4	9.5	1.8	0.413	5.0	0.0A	3.5A	14.0B	5.4	0.068
Ungulates	6.1	8.3	3.2	0.0	1.9	0.380	6.7	11.1	3.9	0.0	2.1	0.353
Garbage[d]	5.2	4.2	4.1	6.5	1.9	0.381						
Non-foods[e]	8.2	4.6	7.8	13.0	1.4	0.499						

[a] Sample sizes are as follows: Annual = 120, Spring = 32, Summer = 56, Autumn = 22.

[b] Sample sizes are as follows: Annual = 107, Spring = 28, Summer = 52, Autumn = 18.

[c] Seasonal values for a food item with a different letter differed ($P < 0.10$).

[d] Includes paper, plastic, aluminum foil, and rubber.

[e] Includes primarily woody debris and sand.

increased through autumn, and use of ants peaked during summer (Table 2). Although seasonal comparisons were not possible, I observed a significant difference ($\chi^2_5 = 35.0$, $P < 0.001$) in the frequency of primary food items in scats between historic and contemporary black bear populations, with greater frequency of insects in black bear diets for the historic population (historic = 44.4%, contemporary = 26.1%; Fisher's exact $P < 0.001$), while grass occurred less frequently (historic = 5.6%, contemporary = 31.5%; Fisher's exact $P < 0.001$) (Table 3).

Corrected for differential digestibility, fecal volume also indicated the same 3 primary food sources annually, though ants became the primary food source (≥ 31.2%; Table 2). Corrected values indicated equivalent volumes of plant (51.0%) and animal (49.0%) food sources in RMNP black bear diets. Corrected use of grasses ($H_2 = 21.8$, $P < 0.001$) again declined from spring through autumn, berry ($H_2 = 10.1$, $P = 0.007$) consumption increased through autumn, while consumption of small mammals ($H_2 = 5.4$, $P = 0.068$) also increased through autumn (Table 2). Scats containing anthropogenic food sources were 15.2 times (Fisher's exact $P < 0.0001$) more common in contemporary black bear diets ($\bar{x} = 14.2\%$; 17 of 120) than in historical black bear diets ($\bar{x} = 0.9\%$; 2 of 214). Because these foods were extremely difficult to identify (i.e., many human foods consist of leftover meat, etc., that leaves no distinct remains), this proportion likely significantly underestimates true occurrence in black bear diets.

I conducted 13, 22, and 4 focal animal observations of black bears during spring, summer, and autumn, respectively, totaling 1,172 minutes ($\bar{x} = 30.1$, SE = 2.7). Observational data indicated similar trends as scat analyses (Table 4). Consumption of grasses was ≥ 5 times greater in spring than summer, while berry (> 100 times) and insect (> 1.3 times) consumption was greater during summer than in spring (Table 4). These same trends continued through

Table 6.3. Comparison of the percent frequency of occurrence of food items in black bear scats from Rocky Mountain National Park, Colorado, between historic (1984–1991) and contemporary (2003–2006) periods. Frequencies included only the most abundant food item per scat.

	Grass	Herbaceous	Berries	Insect	Animal
Historic	5.6A[a]	17.5	22.5	44.4A	10.0
Contemporary	31.5B	11.7	18.9	26.1B	11.7

[a] Percentage frequencies for a food item with a different letter differed ($P < 0.10$).

Table 6.4. Percent time spent foraging on food items based on observations of black bears in Rocky Mountain National Park, Colorado from 2003–2006 for spring (May–June, $n = 13$), summer (July–August, $n = 22$), autumn (September–November, $n = 4$), and all seasons combined ($n = 39$).

	Annual	Spring[a]	Summer	Autumn[b]	*U*	*P*
Grass	17.8	38.9A	8.1B	2.5	253.0	<0.001
Herbaceous	8.1	12.0	6.2	6.0	187.5	0.114
Berries	10.2	0.0A	16.1B	10.9	84.5	0.009
Insects	61.3	49.1A	65.0B	80.6	91.0	0.076
Garbage[c]	2.6	0.0	4.5	0.0		

[a] Significant differences between spring and summer are noted by different letters ($P < 0.10$).

[b] No test was performed for autumn given small sample sizes.

[c] No tests were performed for garbage given only 1 observation of garbage consumption.

autumn, but small sample sizes precluded testing. One direct observation of garbage consumption was noted, further indicating use of anthropogenic foods by black bears in RMNP. No predation events were directly observed, although observations of predation and scavenging were noted by RMNP staff, visitors, and local residents.

GE ($P \leq 0.069$) and FAT ($P \leq 0.041$) in black bear scats were higher during summer than in spring and autumn, whereas spring and autumn did not differ (GE: $P = 0.909$; FAT: $P = 0.749$) (Table 5). FN ($H_2 = 4.3$, $P \geq 0.679$) did not vary across seasons (Table 5). GE was positively related to proportions of ants and ungulates in annual diets, while grasses and herbaceous food items were negatively related (Tables 6 and 7). Similar patterns were present for seasonal diets, although ungulates showed little relationship during summer and autumn (Tables 6 and 7). Interestingly, GE of black bear diets was negatively related to berry consumption during autumn (Table 6). Multivariate models similarly indicated that GE of black bear diets was positively related to the presence of animal matter in black bear diets both seasonally and annually (Table 7), as all bear models indicated positive effects of the variables except for summer diets. Similarly, grass and other herbaceous material either together or separately were associated with lower GE levels in diets in all multivariate models (Table 7), highlighting the proportional lack of contribution of these foods to black bear diet quality.

FAT levels in black bear scats were negatively related to grasses but positively related to berry consumption annually (Tables 8 and 9). This relationship for berries was particularly high during summer and autumn. Although other factors were related to FAT seasonally (Table 8), results were inconsistent among seasons and often counterintuitive (i.e., insects and small mammals having a negative relationship during autumn). The generally weak relationship between FAT and black bear diet composition was highlighted in multivariate models (Table 9),

Table 6.5. Mean values for gross energy (cals), crude fat (%), and fecal nitrogen (%) derived from black bear scats collected in Rocky Mountain National Park, Colorado from 2003–2006 for spring (May–June, $n = 32$), summer (July–August, $n = 55$), autumn (September–November, $n = 20$), and all seasons combined ($n = 107$).

	Annual	Spring[a]	Summer	Autumn	*H*	*P*
Gross energy	5548.7	5441.1A	5656.1B	5425.3A	9.7	0.008
Crude fat	5.5	4.8A	6.2B	4.6A	4.9	0.085
Fecal nitrogen	4.3	4.1	4.4	4.3	4.3	0.119

[a] Seasons not sharing a letter differed ($P < 0.10$).

Table 6.6. Results of simple linear regression comparing gross energy (cals/gm) of black bear scats to the percent volume of foods ingested by black bears in Rocky Mountain National Park, Colorado from 2003–2006. Results are provided for spring (*n* = 34), summer (*n* = 57), and autumn (*n* = 25), as well as all seasons combined (*n* = 123). Significant variables are in bold.

Season	Variable	*F*	*P*	AIC	R^2	β	SE
Annual	**Grass**	22.2	<0.001	1489.5	0.155	–4.788	1.017
	Herbaceous	6.1	0.015	1504.1	0.048	–4.919	1.992
	Berries	0.0	0.940	1510.1	0.000	–0.083	1.096
	Ants	11.5	0.001	1499.0	0.087	3.346	0.987
	Insects	1.2	0.285	1509.0	0.009	1.834	1.709
	Small mammals	0.0	0.986	1510.1	0.000	0.043	2.387
	Ungulates	7.7	0.006	1502.6	0.060	5.194	1.874
Spring	**Grass**	24.3	<0.001	403.9	0.432	–7.314	1.483
	Herbaceous	0.0	0.996	423.1	0.000	–0.017	3.335
	Berries	1.5	0.236	421.6	0.044	5.106	4.225
	Ants	0.9	0.346	422.1	0.028	2.440	2.551
	Insects	0.1	0.747	423.0	0.003	1.618	4.962
	Small mammals	—	—	—	—	—	—
	Ungulates	21.0	<0.001	405.9	0.396	10.675	2.330
Summer	**Grass**	3.7	0.060	692.6	0.063	–3.374	1.754
	Herbaceous	7.7	0.008	688.8	0.123	–10.264	3.702
	Berries	0.4	0.538	695.9	0.007	1.047	1.689
	Ants	1.5	0.233	694.8	0.026	1.668	1.382
	Insects	1.0	0.333	695.3	0.017	2.323	2.376
	Small mammals	0.3	0.609	696.0	0.005	–1.835	3.563
	Ungulates	0.9	0.352	695.4	0.016	4.147	4.422
Autumn	Grass	0.1	0.725	305.7	0.006	–14.729	41.322
	Herbaceous	4.6	0.043	301.3	0.167	–9.866	4.595
	Berries	3.2	0.089	302.6	0.121	–3.076	1.733
	Ants	11.9	0.002	295.4	0.342	6.988	2.023
	Insects	0.0	0.890	305.8	0.001	0.376	2.685
	Small mammals	0.2	0.706	305.7	0.006	1.171	3.061
	Ungulates	0.0	0.897	305.8	0.001	–8.268	63.179

Table 6.7. Results of best multivariate regression models relating gross energy content of black bear scats to the percent volume of foods ingested by black bears in Rocky Mountain National Park, Colorado from 2003–2006. Results are provided for spring (*n* = 34), summer (*n* = 57), and autumn (*n* = 25), as well as all seasons combined (*n* = 123).

			Variables				Model				
Season	Model	Variable	*t*	*P*	β	SE	*F*	*P*	AIC	ΔAIC	R^2
Annual	1	Grass	–3.9	<0.001	–4.113	1.046	12.1	<0.001	1473.8	0.0	0.292
		Herbaceous	–2.8	0.007	–5.025	1.825					
		Ants	2.2	0.027	2.204	0.983					
		Ungulates	2.6	0.010	4.554	1.735					
	2	Grass	–5.1	<0.001	–5.019	0.981	14.0	<0.001	1476.9	3.1	0.261
		Herbaceous	–3.3	0.001	–6.007	1.802					
		Ungulates	2.1	0.041	3.521	1.700					
Spring	1	Grass	–4.1	<0.001	–5.492	1.345	24.0	<0.001	393.3	0.0	0.607
		Ungulates	3.7	0.001	7.629	2.050					
Summer	1	Grass	–2.7	0.011	–4.334	1.637	7.8	0.001	683.9	0.0	0.223
		Herbaceous	–3.3	0.002	–11.924	3.571					
Autumn	1	Herbaceous	–2.6	0.017	–9.422	3.665	10.7	0.001	290.8	0.0	0.494
		Ants	3.8	0.001	6.838	1.814					

Table 6.8. Results of simple linear regression comparing crude fat (%) of black bear scats to the percent volume of foods ingested by black bears in Rocky Mountain National Park, Colorado from 2003–2006. Results are provided for spring (*n* = 34), summer (*n* = 57), and autumn (*n* = 25), as well as all seasons combined (*n* = 123). Significant variables are in bold.

Season	Variable	*F*	*P*	AIC	R^2	β	SE
Annual	**Grass**	6.2	0.014	249.4	0.049	–0.016	0.007
	Herbaceous	1.6	0.211	254.0	0.013	–0.016	0.012
	Berries	21.8	<0.001	235.2	0.153	0.029	0.006
	Ants	1.0	0.311	254.5	0.009	–0.006	0.006
	Insects	0.0	0.910	255.6	0.000	–0.001	0.010
	Small mammals	1.4	0.237	254.1	0.012	–0.017	0.014
	Ungulates	0.7	0.417	254.9	0.006	0.010	0.012
Spring	**Grass**	3.7	0.064	61.3	0.103	–0.018	0.010
	Herbaceous	0.1	0.726	64.9	0.004	0.006	0.017
	Berries	0.2	0.686	64.8	0.005	0.009	0.022
	Ants	1.5	0.233	63.5	0.044	0.016	0.013
	Insects	1.7	0.201	63.2	0.051	–0.033	0.025
	Small mammals	—	—	—	—	—	—
	Ungulates	2.6	0.115	62.3	0.076	0.024	0.015
Summer	Grass	2.7	0.105	122.2	0.047	–0.019	0.012
	Herbaceous	0.3	0.612	124.7	0.005	–0.013	0.026
	Berries	8.7	0.005	116.5	0.137	0.031	0.010
	Ants	6.0	0.018	119.1	0.098	–0.022	0.009
	Insects	1.2	0.288	123.8	0.021	0.017	0.016
	Small mammals	0.0	0.940	124.9	0.000	0.002	0.024
	Ungulates	8.0	0.007	117.2	0.127	0.078	0.028
Autumn	Grass	0.4	0.522	45.3	0.018	–0.147	0.226
	Herbaceous	1.7	0.204	44.0	0.069	–0.035	0.027
	Berries	31.7	<0.001	24.1	0.579	0.037	0.007
	Ants	0.7	0.406	45.0	0.030	–0.011	0.014
	Insects	3.0	0.096	42.7	0.116	–0.024	0.014
	Small mammals	7.7	0.011	38.5	0.252	–0.041	0.015
	Ungulates	1.2	0.295	44.6	0.048	0.364	0.340

Table 6.9. Results of best multivariate regression models relating crude fat content of black bear scats during summer (*n* = 57) to the percent volume of foods ingested by black bears in Rocky Mountain National Park, Colorado from 2003–2006.

			Variables				Model				
Season	Model	Variable	*t*	*P*	β	SE	*F*	*P*	AIC	ΔAIC	R^2
Summer	1	Berries	3.4	0.001	0.033	0.010	10.6	<0.001	108.1	0.0	0.282
		Ungulates	3.3	0.002	0.084	0.025					

which were constructible only for summer diets. This model indicated positive effects of both berries and ungulate biomass on FAT levels of black bear diets.

FN was typically positively related to consumption of animal foods, while increasing amounts of grasses, herbaceous plants, and berries were associated with less FN in black bear scats seasonally and annually (Tables 10 and 11). Regardless of season, insects other than ants were consistently positively associated with FN values, although ants did not exhibit this relationship (Tables 10 and 11). Ungulates were also strongly positively related to FN during spring, while small mammals exhibited a similar response during summer and autumn (Tables 10 and 11). Multivariate models of FN (R^2 = 0.62–0.84) in black bear diets were generally much stronger than models of GE (R^2 = 0.22–0.61) or FAT (R^2 = 0.28), with strongest relationships (i.e., largest β's) in models always associated with animal matter (Table 11).

DISCUSSION

Annual diets of black bears are typically comprised of approximately 85% vegetative matter, with the bulk of animal matter coming from insect sources (Hatler 1972, Raine and Kansas 1990, Hellgren 1993, Pelton 2003). However, relative proportions of vegetative versus animal matter can vary substantially among populations (e.g., southern Yukon = 94.9% vegetative matter, 2.6% animal matter [MacHutchon 1989]; northern Wisconsin = 61.7% vegetative matter, 28.0% animal matter [Payne et al. 1998]). Both historic (insect = 40.0%, vertebrate = 7.7%; Zeigenfuss 2001) and contemporary (insect = 18.9%, vertebrate = 10.0%; Table 2) data from RMNP indicated some of the highest uses of animal matter reported. This was particularly evident when diets were corrected for differential digestibility, as 49.0% of RMNP's contemporary black bear population's diet consisted of animal sources (Table 2). High

Table 6.10. Results of simple linear regression comparing fecal nitrogen (%) of black bear scats to the percent volume of foods ingested by black bears in Rocky Mountain National Park, Colorado from 2003–2006. Results are provided for spring (*n* = 34), summer (*n* = 57), and autumn (*n* = 25), as well as all seasons combined (*n* = 123). Significant variables are in bold.

Season	Variable	*F*	*P*	AIC	R^2	β	SE
Annual	**Grass**	10.7	0.001	257.3	0.082	–0.022	0.007
	Herbaceous	1.6	0.215	266.2	0.013	–0.016	0.013
	Berries	16.9	<0.001	251.7	0.122	–0.027	0.007
	Ants	0.0	0.931	267.7	0.000	0.001	0.007
	Insects	11.9	0.001	256.2	0.089	0.036	0.011
	Small mammals	18.7	<0.001	250.1	0.134	0.062	0.014
	Ungulates	59.7	<0.001	218.4	0.331	0.078	0.010
Spring	**Grass**	8.6	0.006	58.9	0.212	–0.027	0.009
	Herbaceous	0.8	0.368	66.1	0.025	–0.016	0.018
	Berries	1.2	0.288	65.8	0.035	–0.024	0.023
	Ants	0.1	0.783	66.9	0.002	–0.004	0.014
	Insects	3.1	0.088	63.9	0.088	0.044	0.025
	Small mammals	—	—	—	—	—	—
	Ungulates	85.9	<0.001	22.7	0.729	0.077	0.008
Summer	**Grass**	4.2	0.047	82.0	0.070	–0.017	0.008
	Herbaceous	3.3	0.077	82.9	0.056	–0.033	0.018
	Berries	5.2	0.027	81.1	0.086	–0.017	0.008
	Ants	0.0	0.861	86.1	0.001	0.001	0.007
	Insects	15.2	<0.001	72.3	0.216	0.039	0.010
	Small mammals	22.9	<0.001	66.3	0.294	0.068	0.014
	Ungulates	0.3	0.602	85.9	0.005	0.011	0.021
Autumn	Grass	0.2	0.669	60.6	0.008	–0.133	0.307
	Herbaceous	0.6	0.452	60.2	0.025	–0.028	0.037
	Berries	24.4	<0.001	42.8	0.514	–0.047	0.010
	Ants	1.0	0.325	59.7	0.042	0.018	0.018
	Insects	4.0	0.059	56.9	0.147	0.037	0.018
	Small mammals	13.4	0.001	49.3	0.368	0.067	0.018
	Ungulates	0.1	0.804	60.8	0.003	–0.118	0.470

Table 6.11. Results of best multivariate regression models relating fecal nitrogen content of black bear scats to the percent volume of foods ingested by black bears in Rocky Mountain National Park, Colorado from 2003–2006. Results are provided for spring (*n* = 34), summer (*n* = 57), and autumn (*n* = 25), as well as all seasons combined (*n* = 123).

			Variables				Model				
Season	Model	Variable	*t*	*P*	β	SE	*F*	*P*	AIC	ΔAIC	R^2
Annual	1	Grass	–3.5	0.001	–0.016	0.005	51.7	<0.001	132.3	0.0	0.689
		Berries	–4.7	<0.001	–0.021	0.005					
		Insects	5.2	<0.001	0.034	0.007					
		Small mammals	6.8	<0.001	0.061	0.009					
		Ungulates	10.3	<0.001	0.075	0.007					
Spring	1	Insects	5.1	<0.001	0.053	0.010	89.3	<0.001	4.0	0.0	0.843
		Ungulates	12.7	<0.001	0.079	0.006					
Summer	1	Grass	–2.7	0.009	–0.016	0.006	18.8	<0.001	34.7	0.0	0.648
		Herbaceous	–2.0	0.053	–0.024	0.012					
		Berries	–2.9	0.006	–0.015	0.005					
		Insects	4.5	<0.001	0.034	0.007					
		Small mammals	6.1	<0.001	0.065	0.011					
	2	Grass	–2.3	0.026	–0.013	0.006	21.3	<0.001	36.9	2.2	0.621
		Berries	–2.8	0.008	–0.015	0.005					
		Insects	4.8	<0.001	0.036	0.008					
		Small mammals	6.2	<0.001	0.067	0.011					
Autumn	1	Berries	–2.6	0.017	–0.027	0.010	15.4	<0.001	35.8	0.0	0.687
		Insects	1.9	0.074	0.026	0.014					
		Small mammals	3.3	0.003	0.052	0.016					

use of animal matter may be related to the absence of hard mast crops in RMNP. Hard mast crops provide the principal food sources for black bear populations when available (e.g., Hellgren and Vaughan 1988, Costello et al. 2001) because of high energy and fat content (Eagle and Pelton 1983, Inman and Pelton 2002). However, when unavailable, black bears compensate by increasing intake of soft mast and animal matter, as collectively they provide substantial sources of energy, fat, and protein (Swenson et al. 1999, Rode and Robbins 2000, Inman and Pelton 2002; Tables 6–11) that collectively can match or exceed levels attained from hard mast (Kasbohm et al. 1995). However, animal sources are more difficult to find, resulting in increased foraging time (Rode and Robbins 2000) which may be a factor influencing the smaller size of black bears typically associated with areas without high density, high abundance food sources (Welch et al. 1997).

Seasonal diets also vary substantially across geographic localities depending on the food sources that are available. Seasonal use in RMNP appeared to mirror that observed in most other localities that lack natural hard mast sources (e.g., Raine and Kansas 1990, Kasbohm et al. 1995). Green vegetation (grasses and other herbaceous materials) was the primary food source during spring (Table 2) when actively growing early phenology plants show seasonal peaks in protein and digestibility (Pritchard and Robbins 1990). Consumption of grasses decreased over time as crude fiber content increases, resulting in lower protein and digestible energy for simple monogastrics such as black bears (Pritchard and Robbins 1990).

Predation of neonate ungulates and consumption of winter-killed carrion is common during spring for many black bear populations (Irwin and Hammond 1985, Raine and Kansas 1990, Schwartz and Franzmann 1991) and provides much needed protein (Table 10) to replace muscle mass lost during hibernation. Additionally, ungulates provided a greater energy source than green vegetation during spring in RMNP (Table 6). Ungulates were relatively rare in black bear diets in RMNP; thus, although most common in spring diets, the differences were not significant (Table 2). However, ungulate matter was the strongest variable in models of both FN and GE in spring black bear diets, highlighting the importance of ungulates in spring diets, even when relatively rare.

In contrast to ungulates, small mammal consumption increased from spring to autumn (Table 2). As neonate ungulates age, they become substantially more difficult for black bears to capture (Schwartz and Franzmann 1991). Therefore, black bears may have supplemented their diets with small mammals to maintain levels of protein supplied by ungulates during spring, as small mammals were the strongest component associated with FN levels in black bear diets in autumn (Tables 10 and 11).

As with many black bear populations (Raine and Kansas 1990, Noyce et al. 1997), ant consumption peaked in summer (Table 2). Ants provide an important source of protein, fat, and subsequent energy for black bears (Noyce et al. 1997, Swenson et al. 1999, Mattson 2001). Although results from fecal analyses did not indicate a significant positive relationship between ant consumption and either FAT or FN (Tables 8 and 10), ants were the strongest variable in GE content of black bear diets in autumn in RMNP (Tables 6 and 7). Greater digestibility of alates and pupae may have affected summer results, as these life-stages are higher in nutritional value than adults (Noyce et al. 1997, Auger et al. 2004). Greater assimilation of protein and fats from these sources may yield lower values excreted by black bears (Robbins 1993).

Consumption of insects other than ants (primarily wasps) did not differ significantly across seasons (Table 2). Wasp consumption is typically highest during late summer and autumn (Grenfell and Brody 1983, Irwin and Hammond 1985, Holcroft and Herrero 1991), although wasps can provide a significant source of protein annually (Table 10). However, wasp abundance can vary dramatically across years (Graber 1982, Holcroft and Herrero 1991). I observed highest consumption of wasps in 2003 compared to other years (corrected volumetric $\bar{x}$: 2003 = 48.9%, 2004–2006 = 2.1%; Mann–Whitney $U = 768.0$, $P < 0.001$). Because I pooled samples across years to increase sample sizes, these yearly fluctuations may have hidden the relative importance of wasps as a food source when abundant for black bears in RMNP. Unfortunately, sample sizes were too small to effectively test seasonal differences across years.

Berry consumption was greatest during late-summer and autumn (Table 2) when these food items became abundant. Soft mast is typically high in energy content but low in protein (Rode and Robbins 2000). However, I observed the strongest relationship between berry consumption and fecal indices of diet quality with FAT levels in both summer (Tables 8 and 9) and autumn (Table 8). These results were likely influenced by the indigestibility of seeds. Most of the energy associated with berry consumption is in the form of sugars (Rode and Robbins 2000); these are readily utilized by black bears leaving primarily the indigestible seeds and casings to be excreted. These seeds are typically high in fat (Robbins 1993) and likely accounted for the high values I observed. This potentially minimized effects of other foods on FAT, thus resulting in weak and often counterintuitive models of FAT (Tables 8 and 9)

Although consumption of anthropogenic hard mast foods did not differ seasonally, my ability to detect differences was limited given the small number of scats that contained such items ($n = 6$). Additionally, no difference was noted in seasonal use of garbage. However, annual intake of anthropogenic food sources was 15.2 times greater for the contemporary period than the historic. This increased use of human foods may already be manifested in body condition of black bears in my study population (body mass females: historic = 52 kg, contemporary = 58 kg; body fat females: historic = 15.0%, contemporary = 22.8%; see Chapter 2), as anthropogenic food sources yield higher caloric, carbohydrate, protein, and fat intake than most natural diets (Stringham 1989). Use of human-use areas by black bears, where anthropogenic foods are available, was also positively related to black bear condition in RMNP (see Chapter 7). These effects likely resulted in potential population growth rates (historic λ = 1.01, contemporary λ = 1.11; Chapter 4) being much greater in the contemporary population (see Chapter 4). Further, comparisons of the frequency of occurrence of natural food items between historic and contemporary periods suggested higher quality diets historically (i.e., less grass, more insects; Table 3). Therefore, supplementation of anthropogenic foods into black bear diets was likely required to attain the size, condition, and population growth rates exhibited by the contemporary black bear population in RMNP. Unfortunately, this increased use of human foods can also result in negative encounters with humans (Tate and Pelton 1983, Peirce and Van Daele 2006). Historically, black bears in RMNP exhibited cryptic behavior and were believed to avoid heavy human-use areas (McCutchen 1990). However, development along the boundary of RMNP has increased the potential for human-bear encounters (Zeigenfuss 2001). Many black bears in the contemporary population no longer exhibit this avoidance of human-use areas, with home-ranges including many human-use areas (see Chapters 1 and 7). Although current levels of use (5.2% of fecal volume annually; however, it should be noted that this value almost certainly underestimates use of these foods, as common items such as meats, cheese, and processed grains [i.e., bread, donuts, etc.] leave no identifiable residue in scats) are not as high as some other populations (Yosemite National Park, California = 15%, Graber and White 1983; San Gabriel Mountains, California = 33%, Stubblefield 1993), the trend toward increased use parallels that observed in the Lake Tahoe region of Nevada (Beckmann and Berger 2003a, b), which ultimately led to the emigration of most black bears out of wildland areas. Therefore, care should be taken to minimize access to such foods in RMNP.

Focal animal observation corroborated seasonal use patterns seen in scat analyses. Although I was not able to test for differences during autumn, black bears spent significantly less time foraging for grasses during summer than spring, but spent greater time foraging for berries and insects during summer than spring (Table 4). Additionally, I did not directly observe black bears predating or consuming carrion, but have photographs and confirmed observations and reports from RMNP staff, visitors, and local residents of such incidents.

The seasonal variation in fecal GE and FAT was likely driven by differences in dietary composition (Tables 5–11; see above). However, increased fat and carbohydrate assimilation during autumn could also have influenced these values, as well, as Brody and Pelton (1988) found increased assimilation of GE from August to November in 6 captive black bears. Such a physiological change could reduce the amount of energy and fat excreted through waste, which would result in the pattern observed in my data, with similar FAT and GE levels during spring and autumn but higher FAT and GE levels during summer (Table 5). However, Brody and Pelton (1988) believed that increased fat and carbohydrate assimilation comes at the expense of protein assimilation. In contrast, I did not observe any seasonal differences in FN even though diets varied substantially across seasons (Table 2). This suggests that black bears were able to maintain or increase protein consumption annually in RMNP. The strongest relationship to FN levels in black bears shifted from ungulates to small mammals (and, to a lesser degree, insects; Tables 10 and 11) as the year progressed in RMNP, with total corrected ungulate-small mammal-insect consumption peaking at 25.1% of autumn diets (Table 2). Thus, if protein was assimilated less in autumn, FN levels should have risen in RMNP, rather than remaining similar. Differing assimilation efficiencies must be further explored before a clearer understanding can be obtained.

MANAGEMENT IMPLICATIONS

Black bears in RMNP utilize grasses and other herbaceous plants extensively during spring and early summer, but nutritional gains from these resources were minimal compared to animal matter. Conversely, vertebrate consumption comprised < 12% of black bear diets annually in RMNP, yet provides a valuable source of protein and energy for the population. Maximizing foods high in energy, protein, and fat would likely benefit the local black bear population, but remains difficult given the high elevation of RMNP and the park's "natural regulation" philosophy. Because plant material is much more abundant, maintaining high quality herbaceous forage habitats is important in RMNP. Because most use of grasses occur in spring, current prescribed burning practices and letting wildfires burn to the extent possible could provide early successional habitats as well as increase biomass, speed green-up, and increase nutritional quality of black bear diets because of decreased canopy cover, released nitrogen from ground litter, and warming of microclimate for faster green-up (Neary et al. 1999). Similarly, dead and down ground cover (i.e., fallen logs from dead trees) could increase post-fire, providing abundant logs and cover for ants, other insects, and small mammals (Noyce et al. 1997, Suzuki and Hayes 2003).

Additionally, RMNP staff has proposed several alternatives for reducing elk numbers in RMNP (National Park Service 2006). Such a reduction in herd size could reduce available ungulate biomass, particularly in spring, due to loss of winter-killed carrion and fewer neonates and warrants future monitoring given the importance of ungulates as a protein and energy source in spring diets. If insufficient numbers are available, black bears will likely need to compensate by switching to other high protein-high energy sources (i.e., small mammals, insects, etc.). Lastly, I have noted a shift in black bear use away from wildlands into human-wildland interface areas (see Chapters 1 and 7). This shift, combined with increased use of anthropogenic foods by black bears over the last 15–20 years, warrants further monitoring given the propensity of black bear populations to habituate to urban settings (Beckmann and Berger 2003a, b), frequently resulting in conflicts detrimental to local black bear populations.

LITERATURE CITED

Agresti, A. 1996. An introduction to categorical data analysis. John Wiley and Sons, New York, New York, USA.

Auger, J., G. L. Ogborn, C. L. Pritchett, and H. L. Black. 2004. Selection of ants by the American black bear (*Ursus americanus*). Western North American Naturalist 64:166–174.

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, New Mexico, USA.

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

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

Brody, A. J., and M. R. Pelton. 1988. Seasonal changes in digestion in black bears. Canadian Journal of Zoology 66:1482–1484.

Bunnell, S. T. 2000. Spring and summer diet and feeding behavior of black bears on the East Tavaputs Plateau, Utah. Thesis, Brigham Young University, Provo, Utah, USA.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.

Clark, J. E., J. L. Parsons, E. C. Hellgren, E. E. Jorgensen, and D. M. Leslie, Jr. 2003. Nitrogen concentration of stomach contents as an index of dietary nitrogen for *Sigmodon hispidus*. Journal of Mammalogy 84:1399–1409.

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, New Mexico, USA.

Eagle, T. C., and M. R. Pelton. 1983. Seasonal nutrition of black bears in the Great Smoky Mountains National Park. International Conference on Bear Research and Management 5:94–101.

Elowe, K. D., and W. E. Dodge. 1989. Factors affecting black bear reproductive success and cub survival. Journal of Wildlife Management 53:962–968.

Feucht, J. R. 1999. Illustrated guide to trees and shrubs of Rocky Mountain National Park. Kopy Kat Graphics and Printing, Granby, Colorado, USA.

Gluesing, E. A., and D. M. Field. 1986. Limitations of existing food-habit studies in modeling wildlife-habitat relationships. Pages 251–253 *in* J. Verner, M. L. Morrison, and C. J. Ralph, editors. Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. University of Wisconsin Press, Madison, Wisconsin, USA.

Graber, D. M. 1982. Ecology and management of black bears in Yosemite National Park. Technical report Number 5 to National Park Service. Institute of Ecology, University of California at Davis, USA.

Graber, D. M., and M. White. 1983. Black bear food habits in Yosemite National Park. International Conference on Bear Research and Management 5:1–10.

Grenfell, W. E., Jr., and A. J. Brody. 1983. Seasonal foods of black bears in Tahoe National Forest, California. California Fish and Game 69:132–150.

Hatler, D. F. 1972. Food habits of black bears in interior Alaska. Canadian Field-Naturalist 86:17–31.

Hellgren, E. C. 1993. Status, distribution, and summer food habits of black bears in Big Bend National Park. The Southwestern Naturalist 38:77–80.

Hellgren, E. C., and M. R. Vaughan. 1988. Seasonal food habits of black bears in Great Dismal Swamp, Virginia-North Carolina. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 42:295–305.

Herrero, S. 2002. Bear attacks-their causes and avoidance. The Lyons Press, Guilford, Connecticut, USA.

Hewitt, D. G., and C. T. Robbins. 1996. Estimating grizzly bear food habits from fecal analysis. Wildlife Society Bulletin 24:547–550.

Hodgman, T. P., B. B. Davitt, and J. R. Nelson. 1996. Monitoring mule deer diet quality and intake with fecal indices. Journal of Range Management 49:215–222.

Holcroft, A. C., and S. Herrero. 1991. Black bear, *Ursus americanus*, food habits in southwestern Alberta. Canadian Field Naturalist 105:335–345.

Holechek, J. L., R. D. Pieper, and C. H. Herbel. 2004. Range management: principles and practices. Pearson Education, Upper Saddle River, New Jersey, USA.

Inman, R. M., and M. R. Pelton. 2002. Energetic production by soft and hard mast foods of American black bears in the Smoky Mountains. Ursus 13:57–68.

Irwin, L. L., and F. M. Hammond. 1985. Managing black bear habitats for food items in Wyoming. Wildlife Society Bulletin 13:477–483.

Kasbohm, J. W., M. R. Vaughan, and J. G. Kraus. 1995. Food habits and nutrition of black bears during a gypsy moth infestation. Canadian Journal of Zoology 73:1771–1775.

Leslie, D. M., Jr., and E. E. Starkey. 1985. Fecal indices to dietary quality of cervids in old-growth forests. Journal of Wildlife Management 49:142–146.

MacDonald, D. W., P. D. Stewart, P. Stopka, and N. Yamaguchi. 2000. Measuring the dynamics of mammalian societies: an ecologist's guide to ethological methods. Pages 332–388 *in* L. Boitani and T. K. Fuller, editors. Research techniques in animal ecology: controversies and consequences. Columbia University Press, New York, New York, USA.

MacHutchon, A. G. 1989. Spring and summer food habits of black bears in the Pelly River Valley, Yukon. Northwest Science 63:116–118.

Magomedov, M. R. D., S. M. Gasanova, and M. G. Khashaeva. 1996. Relationship between the qualitative compositions of food resources, stomach contents, and feces in small herbivorous mammals. Russian Journal of Ecology 27:339–344.

Mattson, D. J. 2001. Myrmecophagy by Yellowstone grizzly bears. Canadian Journal of Zoology 79:779–793.

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.

McDonald, J. E., Jr., and T. K. Fuller. 1994. Black bear food habits: beyond the same old scats. Proceedings of the International Congress of Game Biologists 21:293–298.

McLean, P. K., and M. R. Pelton. 1990. Some demographic comparisons of wild and panhandler bears in the Smoky Mountains. International Conference on Bear Research and Management 8:105–112.

Moore, T. D., L. E. Spence, and C. E. Dugnolle. 1974. Identification of the dorsal guard hairs of some mammals of Wyoming. Wyoming Game and Fish Department, Laramie, Wyoming, USA.

Morrison, M. L., B. G. Marcot, and R. W. Mannan. 1992. Wildlife-habitat relationships: concepts and applications. First edition. The University of Wisconsin Press, Madison, Wisconsin, USA.

National Park Service. 2006. Draft Environmental Impact Statement/Elk and Vegetation Management Plan. Unpublished report. U.S. National Park Service, Rocky Mountain National Park, Colorado, USA.

Neary, D. G., C. C. Klopatek, L. F. DeBano, and P. F. Ffolliott. 1999. Fire effects on belowground sustainability: a review and synthesis. Forest Ecology and Management 122:51–71.

Noyce, K. V., P. B. Kannowski, and M. R. Riggs. 1997. Black bears as ant-eaters: seasonal associations between bear myrmecophagy and ant ecology in north-central Minnesota. Canadian Journal of Zoology 75:1671–1686.

Payne, N. F., B. E. Kohn, N. C. Norton, and G. G. Bertagnoli. 1998. Black bear food items in northern Wisconsin. Transactions of the Wisconsin Academy of Sciences, Arts and Letters 86:263–280.

Peirce, K. N., and L. J. Van Daele. 2006. Use of a garbage dump by brown bears in Dillingham, Alaska. Ursus 17:165–177.

Pelton, M. R. 2003. Black bear (*Ursus americanus*). Pages 547–555 *in* G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, editors. Wild mammals of North America: biology, management, and conservation. Second edition, revised. The Johns Hopkins University Press, Baltimore, Maryland, USA.

Pritchard, G. T., and C. T. Robbins. 1990. Digestive and metabolic efficiencies of grizzly and black bears. Canadian Journal of Zoology 68:1645–1651.

Raine, R. M., and J. L. Kansas. 1990. Black bear seasonal food habits and distribution by elevation in Banff national Park, Alberta. International Conference on Bear Research and Management 8:297–304.

Robbins, C. T. 1993. Wildlife feeding and nutrition. Second edition. Academic Press, San Diego, California, USA.

Rode, K. D., and C. T. Robbins. 2000. Why bears consume mixed diets during fruit abundance. Canadian Journal of Zoology 78:1640–1645.

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.

Rosas-Rosas, O. C., R. Valdez, L. C. Bender, and D. Daniel. 2003. Food habits of pumas in northwestern Sonora, Mexico. Wildlife Society Bulletin 31:528–535.

Schwartz, C. C., and A. W. Franzmann. 1991. Interrelationship of black bears to moose and forest succession in the northern coniferous forest. Wildlife Monographs 113.

Stringham, S. F. 1989. Demographic consequences of bears eating garbage at dumps: an overview. Pages 35–42 *in* M. Bromley, editor. Bear–people conflicts—Proceedings of a symposium on management strategies. Northwest Territories Department of Renewable Resources, Yellowknife, Northwest Territories, Canada.

Stubblefield, C. H. 1993. Food habits of black bear in the San Gabriel Mountains of southern California. The Southwestern Naturalist 38:290–293.

Suzuki, N., and J. P. Hayes. 2003. Effects of thinning on small mammals in Oregon coastal forests. Journal of Wildlife Management 67:352–371.

Swenson, J. E., A. Jansson, R. Riig, and F. Sandegren. 1999. Bears and ants: myrmecophagy by brown bears in central Scandinavia. Canadian Journal of Zoology 77:551–561.

Tate, J., and M. R. Pelton. 1983. Human-bear interactions in Great Smoky Mountains National Park. International Conference on Bear Research and Management 5:312–321.

Welch, C. A., J. Keay, K. C. Kendall, and C. T. Robbins. 1997. Constraints on frugivory by bears. Ecology 78:1105–1119.

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

Zardus, M. J., and D. J. Parsons. 1980. Black bear management in Sequoia and Kings Canyon National Parks. International Conference on Bear Research and Management 4:195–200.

Zeigenfuss, L. C. 2001. Ecology of black bears in Rocky Mountain National Park: an analysis of population dynamics, diet, and habitat selection (1985–1991). Unpublished report, U.S. National Park Service, Rocky Mountain National Park, Colorado, USA.

Chapter 7:

Determination of critical habitats of black bears in Rocky Mountain National Park, Colorado

Roger A. Baldwin, Department of Animal and Range Sciences, New Mexico State University, P.O. Box 30003 MSC 4901, Las Cruces, New Mexico 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, New Mexico 88003, USA

Chapter summary: Black bears (*Ursus americanus*) are rare in Rocky Mountain National Park (RMNP), Colorado (20–24 bears), and understanding habitat components critical to their productivity and survival is essential in maintaining such a low density population. We assessed habitat selection across 3 spatial scales (landscape, home-range, and site-specific) to delineate critical habitats for black bears in RMNP for both historic (1984–1991) and contemporary (2003–2006) populations to identify critical habitats and see if these changed over time. Black bear habitat selection at both landscape and home-range scales was highly variable both historically and contemporarily, although commonly included preference for aspen covertypes and human-use sites and avoidance of open covertypes. Relationships were more consistent for landscape metrics, with black bears preferring highly diverse landscapes high in edge and comprised of small patches both in the historic and contemporary periods. Nutritional condition of black bears in RMNP was most strongly positively associated with aspen, mesic shrublands, and human-use areas, while limber pine and mixed conifer had the most consistent negative influence on bear body fat and body condition indices. Human-use areas were also used at a much higher rate contemporarily (70% of black bear locations in human-use areas) than historically (51% of black bear locations in human-use areas), suggesting increasing habituation of black bears for human influenced habitats. This trend likely was driven by high yield resource capture (i.e., anthropogenic food sources) which may explain increased size and productivity of black bears in RMNP. Site-specific analyses indicated that black bears preferred north and east facing aspects, greater numbers of logs and ant mounds, and less grass and woody cover at foraging sites as compared to random sites. Site-specific preferences correspond to habitat attributes that predict greater quantity and quality of plant and insect foods for black bears. Few differences were found between resting and foraging locations. However, observed differences indicated a preference for steeper slopes and denser woody understory cover at resting sites. Both of these attributes relate to less disturbance and greater security. Black bears in RMNP likely use areas proving the greatest security within foraging sites for resting locations. Collectively, analyses suggested that small, evenly distributed patches of aspen, human-use, and mesic shrubland covertypes provided the best habitat for black bears in RMNP. Covertype composition was likely less important than high habitat diversity, however, as black bear distribution patterns were tied closely to actual distribution of food sources that show high annual, seasonal, and spatial variability in RMNP. By maximizing diversity within home-ranges, black bears likely assure that at least some components associated with important foods will be present in home-ranges. Management strategies designed to provide or increase the diversity of RMNP's landscape and provide key structures associated with black bear foraging (i.e., dead and

down logs, etc.) may help reverse an apparent shift in bear use to high human-use sites while maintaining good bear body condition in RMNP.

———————

Rocky Mountain National Park (RMNP) conserves a small population of black bears (*Ursus americanus*) of uncertain ecological status (20–24 individuals, see Chapter 3). Virtually every survival and reproductive demographic of large mammals is related to energy balance of individuals; body reserves are gained through nutrition and lost through daily activities and disturbance (Hanks 1981, Franzmann 1985, Rogers 1987, Gaillard et al. 2000, Bender and Cook 2005, Bender et al. 2007a, b, c; Lomas and Bender 2007). Both nutrition and security are critical habitat attributes and fundamentally related to individual condition (Davis 2006, Bender et al. 2007c); thus, habitat is critical for survival and productivity of black bears. Despite small population size, little is known of habitats critical to black bear survival or productivity in RMNP. Because of this, RMNP staff has concerns over the viability of the black bear population, preservation of which is a key management goal of the National Park Service (National Park Service 1988).

Historic data collected from 1984–1991 indicated that RMNP's black bear population was unique, as it had one of the lowest densities and reproductive rates ever recorded (see Chapters 3 and 4; Zeigenfuss 2001). Additionally, black bear size was well below average and home-range sizes were much larger than typical (especially for females; see Chapter 2; Zeigenfuss 2001). These characteristics (small individual size, low productivity, large home ranges) are all indicators of habitats providing limited nutrition (Hanks 1981, Rogers 1987, McLoughlin et al. 2000). RMNP is comprised almost entirely of tundra, high elevation forests, and meadows; such habitats generally lack hard mast crops, and soft mast crops can be scarce and variable. Moreover, potential food sources for black bears are limited, and high elevations

(> 2,286 m) result in short growing seasons (6–7 months/year active), limiting the time that black bears have to obtain resources necessary for growth and reproduction. These characteristics suggest that habitats of RMNP may be of low quality for black bears. Because of the importance of nutrition for survival and productivity of wildlife populations (Hanks 1981, Cook et al. 2001, Noyce et al. 2002, Lomas and Bender 2007, Bender et al. 2007a, b), possible plant composition and growth limitations in RMNP habitats makes it important to identify key bear use areas and critical foraging and security areas. Disturbance to or loss of these critical areas could strongly affect survival and productivity of RMNP's black bear population. Because review of historic demographics (see Chapter 4; Zeigenfuss 2001) suggested that the black bear population in RMNP was barely able to balance mortality with recruitment, loss of critical areas could lower survival and productivity and could result in the loss of black bears from RMNP or lead to increased use of areas outside RMNP boundaries.

Additionally, increased development of wildland areas surrounding RMNP (Zeigenfuss 2001) and potential habituation to humans could yield an altered dynamic between RMNP's black bear population and habitat/landscape components (Herrero 1983, Rogers 1987, Beckmann and Berger 2003a, b). Such effects were seen with increasing development in the Lake Tahoe region of Nevada (Beckmann and Berger 2003a, b), and resulted in increased use of human-associated habitats and anthropogenic food sources. Shifts into human-use areas could result in greater property damage (Peirce and Van Daele 2006); higher mortality rates from hunting (Samson and Huot 1998), vehicular collisions (Beckmann and Berger 2003b, Freedman et al. 2003), and removal of problem bears (McCarthy and Seavoy 1994); and potentially the decline of RMNP's black bear population due to emigration out of wildland areas (Beckmann and Berger 2003a, b). Therefore, understanding the influence of both natural and anthropogenic habitat attributes on use, survival, and productivity parameters is necessary to effectively manage RMNP's black bear population.

Habitat selection of most large mammals typically focuses on 3 scales: 1) selection of an individuals home-range within the landscape (hereafter landscape); 2) selection of different habitat patches within the home-range (hereafter home-range); and 3) selection of site specific areas (i.e., feeding and resting sites; hereafter site-specific; Johnson 1980, Lofroth 1993). These different levels reflect the hierarchical nature of resource selection (Johnson 1980, Aebischer et al. 1993, Anderson and Gutzwiller 1996). Because selection can occur at multiple scales, understanding habitat use patterns in the context of spatial scale is only relevant after examining habitat use across multiple scales (O'Neill et al. 1988, Kotliar and Wiens 1990, Lord and Norton 1990, Apps et al. 2001).

Additionally, the fractal nature of landscapes can influence the perception of habitat components across various scales (O'Neill et al. 1988, Ritchie 1998). The fractal nature of many landscapes results from varying sizes and distributions of resource patches. This fractal nature is at the heart of habitat selection, as the scale at which an individual perceives the environment influences how habitat factors are perceived and the abundance of resources it detects (O'Neill et al. 1988, With 1994, Ritchie 1998). For example, a black bear may perceive a given fractal habitat as having only a few large patches or it may perceive this same habitat as having many small patches nested within one to several larger patches (Wiens 1989, Ritchie 1998). Therefore, an understanding of how black bears are selecting patches should result in more efficient habitat models that link habitat-use patterns across hierarchical levels of selection.

The importance of different scales varies among species. Landscape level features can be the overriding factor in determining habitat suitability of some animals [e.g., spotted owl (*Strix* *occidentalis*); Hansen et al. 1993] while smaller-scale factors are more important for others [e.g., bison (*Bison bison*), Fortin et al. 2003; elk (*Cervus elaphus*), Jones and Hudson 2002]. However, the more likely result is selection at multiple scales, resulting in a hierarchy that explains selection at progressively higher or lower levels (Pedlar et al. 1997, Jones and Hudson 2002, Weir and Harestad 2003). Few studies have assessed habitat use by black bears across multiple scales (Clark et al. 1993, Lyons et al. 2003); such a hierarchy should allow for greater understanding of relationships between site-specific parameters and stand and/or landscape components resulting in more effective and applicable models of habitat selection and consequently development of more effective conservation strategies (Mysterud et al. 1999, Weir and Harestad 2003).

To determine habitats in RMNP that are critical to black bear survival and productivity, I assessed habitat use across 3 spatial scales (landscape, home-range, site-specific). Because habitat quality fundamentally relates to quantities of body reserves black bears can accrue, I related important habitat attributes to various indices of bear condition, including percent body fat and a body condition index. Last, I related black bear locations from 1984–1991 (hereafter, historical period) and 2003–2006 (hereafter, contemporary period) to human-use areas to assess differences in use of such areas over time. My goal was to identify which habitat components of RMNP best provided for fundamental needs of black bears, and to assess whether these factors have changed over time.

METHODS

Capture and radiotracking

I used modified Aldrich foot snares and culvert traps to capture black bears from 1984–1991 and 2003–2006. I immobilized bears with a 5:1 mixture of ketamine hydrochloride and xylazine hydrochloride (200 mg ketamine and 40 mg xylazine per ml) and fit bears with radiocollars. I radiotracked individuals from capture through the time of den entrance, and subsequently from May through den entrance annually. I obtained fixes of bears as often as possible, with locations typically recorded a minimum of once per week. However, due to logistical constraints and movements off RMNP property, the time interval between locations was occasionally longer. I used locations to construct 95% minimum convex polygon (MCP) annual home-ranges (see Chapter 1) for habitat analyses. Most fixes were within 200 m of the bear's location (1984–1991 = 83%; 2003–2006 = 84%), with direct observations recorded when possible from 2003–2006 for use in site-specific analyses.

Landscape

I estimated 16 annual home-ranges for 9 (5 females, 4 males) black bears from 1984–1991 and 21 annual home ranges for 10 (6 females, 4 males) black bears from 2004–2006 (see Chapter 1). Historically, 11 home-ranges were east of the continental divide while 5 were west. Contemporarily, 20 home-ranges were east of the divide with only 1 in western RMNP. I randomly placed an additional 100 circular simulated home-ranges throughout RMNP for comparison to actual home-ranges. I used the mean size of an adult female black bear's home-range in RMNP as the size of simulated home-ranges (95% MCP = 32.2 km^2; see Chapter 1). Although the shape of the home-range can influence landscape metrics, this difference was negligible for a similar study with American martens (*Martes americana*; Potvin et al. 2001) and

I assumed this would not influence these factors in this study. I extracted habitat attribute data from GIS coverages of RMNP (Salas et al. 2005) and surrounding areas provided by RMNP staff, and used forest covertypes (Table 1) and 7 landscape metrics (Table 2) to model black bear landscape use. I selected landscape metrics based on their depiction of important landscape factors for bears (Linke et al. 2005). I also created a 400 m buffer around all human-use areas (trails, roads, campsites, and other developed areas) to assess their impact on black bear occurrence at the landscape and home-range scales and included these areas in covertype analyses. I calculated all landscape variables using the Patch Analyst extension (Elkie et al. 1999) in ArcView 3.3 (Environmental Systems Research Institute, Redlands, California, USA).

I used logistic regression (Hosmer and Lemeshow 2000) to assess univariate associations ($\alpha = 0.10$) to home-range composition and associated landscape metrics for each variable individually between actual and randomized home-ranges. I used Spearman rank correlations to assess collinearity among variables; if variables were correlated at $r_s \geq 0.70$, only the variable with the lower Schwartz information criteria (SIC) value was included in further analyses to reduce redundancy (Agresti 1996) unless correlated variables had no functional relationship to each other. Once the data set was reduced, I constructed univariate and multivariate models using logistic regression, and used the χ^2 score statistic (Hosmer and Lemeshow 2000) to determine the 16 highest scoring models for each level of model parameter size (i.e., 1 through the highest number of parameters in the reduced data set). I compared resultant models using SIC differences (ΔSIC) to determine only those habitat factors most strongly related to occurrence (Link and Barker 2006). I considered only models with ΔSIC's < 4 competing models, and used maximum rescaled generalized R^2 values (Nagelkerke 1991) and concordance (con) to aid in model selection (Hosmer and Lemeshow 2000). For each model selection criteria,

Table 7.1. Covertypes used to construct black bear habitat models for Rocky Mountain National Park, Colorado. Covertypes were derived from vegetation classification maps of RMNP and surrounding areas (Salas et al. 2005).

Covertype	Description
Herbaceous meadow	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/fir species along riparian or seasonally flooded areas
Mixed conifer	Characterized by codominance of two or more 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 can be codominant
Rock	Characterized by rock, bare soil, or snow
Non-vegetated surface	Included areas covered by roads, trails, and campsites

Table 7.2. Landscape metrics and associated descriptions related to black bear occurrence in Rocky Mountain National Park, Colorado.

Variable	Description
Patch density	Number of patches/km^2
Edge density	Meters of edge/ha
Shannon’s diversity index	Measure of relative patch diversity
Shannon’s evenness index	Measure of patch distribution and abundance
Total number of patches	Total number of patches summed for all covertypes
Area-weighted mean shape index	Measure of shape complexity
Interspersion juxtaposition index	Measure of patch adjacency

I assigned the best model (i.e., lowest SIC score, highest R^2, and highest concordance) a rank of 1, with each successive model ranked incrementally lower. I considered only models with R^2 and concordance differences < 10% equally supported. I summed ranks for all model selection criteria and chose the model with the lowest sum as the best supported model (Lomas and Bender 2007). In case of a tie in rankings, I chose the more parsimonious model. I used odds ratios to interpret relationships of habitat factors to landscape selection, and multiplied Shannon's evenness index by 100 to facilitate this interpretation. Because I compared black bear home-ranges to randomly generated home-ranges, as opposed to areas of known absences, primary emphasis of results was placed on odds ratios and the relative ranking of habitat components rather than on predicting overall probability of use (Keating and Cherry 2004). Similarly, multivariate models were primarily developed to validate the consistency of direction of habitat components (i.e., either positive or negative) for black bears rather than to predict absolute relationships between variables.

I conducted separate analyses for home-ranges east of the continental divide, west of the divide, and collectively for both sides for the historic period; analyses were conducted only for the east side and for both sides combined during the contemporary period given the lack of home-ranges west of the continental divide. For collective analyses of both sides of RMNP, I used all 100 random home-ranges, while for separate analyses for eastern and western localities, I used 50 random home-ranges.

I also used occupancy modeling to provide an alternative approach for assessing habitat selection at the landscape scale. This approach incorporates imperfect detection of black bears at remote-sensored camera sites (see Chapter 3 for survey protocol) and results in an unbiased occupancy model (MacKenzie et al. 2005). Additionally, occupancy modeling allows the user to incorporate habitat variables in the form of covariates to assess habitat features influencing occupancy (MacKenzie et al. 2005). I related black bear occurrence at camera sites to covertypes and landscape metrics at the home-range scale through the use of a 32.2 km^2 sampling window around the camera location and used data collected within this buffer in subsequent analyses. I selected this window size to represent the average home-range size of female black bears in RMNP (see Chapter 1). For occupancy analyses, I used the same variables used in the logistic regression analyses. Also, camera sites were separated into western and eastern subdivisions of RMNP to assess large-scale differences in precipitation and associated vegetative communities caused by orographic lift of air masses between the separate sides. For occupancy analyses, I used model 1 (assumes Markovian changes in occupancy) in program PRESENCE (MacKenzie et al. 2003). All model selection procedures followed those listed above for logistic regression analyses. However, because camera trapping was conducted in late summer and autumn, and black bear distribution and habitat preference may change seasonally (Pelton 2003), I limited interpretations of occupancy models to a seasonal context.

Home-range

For known locations (either visually observed, heard foraging or moving, or observed foraging or resting sign from a radiocollared bear that was disturbed through tracking efforts) from the contemporary period, I determined the proportion of use (total number of locations per covertype/total number of locations per home-range) of covertypes (see Table 1) and human-use areas (within 400-m buffer of campsites, roads, and trails) for each individual and subtracted this value from the proportion of covertypes available within each home-range. I took these differences for each bear and randomly selected with replacement (bootstrapped; Efron and Tibshirani 1993) $N = 1{,}000$ combinations of difference values. I used the $N = 1{,}000$ mean difference values from each bootstrap replicate to create a frequency distribution of differences, and ranked the frequency distribution to exclude the extreme 50 values from each tail to develop 90% bootstrap CIs. If the CI included 0, bears were distributed randomly with respect to that covertype. For all covertypes non-randomly utilized (CI did not include 0), I calculated selection ratios (percent use/percent availability) to express selection for or against covertypes (Bender et al. 2007b). I conducted these procedures for both annual and seasonal home-ranges. Additionally, I used Fisher's exact test (Zar 1999) to test differences in bear presence in human-use sites between historic and contemporary periods. I did not conduct bootstrap analyses on historic data given the small number of data points collected annually and seasonally for most black bears from this time period and uncertainty of covertypes associated with many locations.

Additionally, I used Maximum Entropy (MaxEnt, version 3.1) modeling (Phillips et al. 2006) to estimate the influence of habitat types (Table 1), height of canopy (height of the dominant overstory classed as 0 = no canopy, 1 = <1 m, 2 = 1–5 m, 3 = 5–15 m, 4 = 15–30 m, and 5 = >30 m), elevation (m), degree of slope, aspect (north = 316º–45º, east = 46º–135º, south = 136º–225º, and west = 226º–315º), and distance to nearest roads (m) and trails (m) on known black bear locations from the contemporary period. This approach utilizes only observed locations (i.e., presence) to determine important habitat attributes, and has the advantage of using random background locations for comparative points rather than requiring the use of known absence locations for comparative sites (Phillips et al. 2006). As such, MaxEnt modeling can provide a less biased alternative to other approaches that require the generation of non-use locations (i.e., discriminant analysis, logistic regression) when it is unknown if such sites are truly unused (Phillips et al. 2006).

For this approach, I constructed 95% MCP home-ranges (see Chapter 1) for each bear for which I had a minimum of 15 known locations. I compared these known locations to 10,000 random background points within each bear's respective home-range using MaxEnt modeling procedures. I used receiver operating characteristic (ROC) plots to assess relative performance of models and to establish thresholds for identifying the viability of a site for use by each bear (Phillips et al. 2006). The ROC is a plot of sensitivity and 1 – specificity, with sensitivity representing how well the data correctly predicts presence while specificity provides a measure of correctly predicted absences (Fielding and Bell 1997). I also used the area under curve (AUC) approach to assist in selecting the most appropriate model (Fielding and Bell 1997, Phillips et al. 2006). This approach provides an index of model accuracy; values range from 0.5–1.0 with values of 0.5 indicating no fit greater than that expected by chance. Standard errors were calculated for AUC values using 30% of locations as test data (Phillips et al. 2006). Often, AUC values are greatest for models with many variables, though certain variables may add little to the model. Therefore, I used a critical ratio test (Pearce and Ferrier 2000) to compare the model with the highest AUC to simpler models to determine if the increase in explanatory value was significant at $\alpha = 0.05$. Because models were constructed using the same evaluation data, I calculated Spearman rank correlation coefficients (r_s) between competing models. In contrast to Pearce and Ferrier (2000), I could only construct correlations for known locations as I lacked absence data. I then incorporated r_s into the critical ratio test (Pearce and Ferrier 2000) using the following:

$$Z = \frac{A_1 - A_2}{\sqrt{SE_{A_1}^2 + SE_{A_2}^2 - 2 r_s \, SE_{A_1} SE_{A_2}}}$$

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, I selected the more parsimonious model as my preferred model.

For each model, MaxEnt calculates the relative percent contribution of each variable. This value provides 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, personal communication). I compared the percent contribution of each variable in the preferred models of individual bears using a Kruskal–Wallis test (Zar 1999) to determine collectively which variables were most influential in predicting black bear occurrence. I then included all significant habitat variables in a final MaxEnt model to collectively illustrate the influence of those factors on black bear distributions in RMNP. By constructing models separately for each bear to determine habitat variables most influencing bear distribution, I was able to use the bear as the replicate rather than each location.

Additionally, I derived thresholds for probability of use for test data by maximizing sensitivity and minimizing specificity (Fielding and Bell 1997, Phillips et al. 2006). I used these thresholds to convert probabilities to binary responses (presence-absence). For my study, I used the equal test sensitivity and specificity threshold to calculate a classification percentage (number of test locations with predicted probabilities greater than the threshold value/the total number of test locations) to corroborate results from the ROC curve for the final model.

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 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 relationship, and the magnitude of these movements indicates the strength of these relationships.

I also modeled historic use of habitat components by black bears in RMNP to assess potential changes over time. Because I was uncertain of the precision of some historic location data, I only used locations with estimated error terms of ≤ 200 m to most accurately define habitat use by black bears while providing a sufficient number of locations for analyses. Nonetheless, I acknowledge that historic locations may have been less precise than contemporary locations and could bias results; thus, I only used results for general comparisons between historic and contemporary populations. I extracted all habitat attribute data used in MaxEnt models from GIS layers of RMNP and surrounding areas (Salas et al. 2005) using ArcView 3.3 (Environmental Systems Research Institute, Redlands, California, USA).

Site-specific

I selected 15 structural, physiographic, and cover variables (Table 3) to relate to observed foraging and resting locations of radiocollared black bears. The actual location of bears served as the plot center, and I established 4 25-m transects radiating from the plot center at 90° intervals with the initial direction chosen at random. I used the point intercept method (Levy and Madden 1933) to assess percent cover for the area and identified all vegetation to species when possible. For analyses, I combined all points into 7 categories: 1) logs, 2) fruit producing species, 3) ant mounds and rocks with ants underneath, 4) woody species, 5) grasses, 6) herbaceous plants, and 7) non-vegetated surfaces (i.e., large boulders, duff layer, water, etc.). I assessed slope in degrees at plot center and at the end of each radial transect and averaged these

Table 7.3. Means, standard errors (SE), and associated results of Mann–Whitney *U*-tests[a] comparing habitat characteristics measured at foraging ($n = 35$) and resting ($n = 8$) sites of black bears in Rocky Mountain National Park, Colorado during 2005–2006. Significant variables are in bold.

	Foraging		Resting			
Variable	$\bar{x}$	SE	$\bar{x}$	SE	χ^2	*P*
Canopy cover	57.6	4.2	68.6	4.7	1.33	0.248
Vertical cover	45.1	3.9	50.5	8.8	0.25	0.618
Canopy height	7.7	0.6	8.5	0.6	0.17	0.685
Stem density	12.3	1.3	10.4	2.6	0.43	0.512
Basal area trees	26.3	3.4	21.2	2.9	0.32	0.574
Basal area snags	10.9	1.8	10.7	4.6	0.01	0.937
Slope	18.6	1.3	25.4	3.5	3.00	0.083
Aspect[b]					3.59	0.310
Ants	1.1	0.3	0.4	0.3	0.72	0.396
Logs	7.0	1.1	5.1	1.4	0.37	0.541
Grass	7.1	1.9	6.6	3.3	0.03	0.871
Fruits	18.5	3.1	16.8	2.6	0.33	0.563
Woody	3.3	0.6	11.0	4.1	4.09	0.043
Herbaceous	10.4	2.1	14.1	6.1	1.19	0.276
Non-vegetated	52.6	4.5	46.0	5.3	0.35	0.553

[a] χ^2 approximation statistic listed for comparison to χ^2 analysis of aspect.

[b] Categorical variable analyzed using χ^2 test. Number of locations in each class for foraging (F) and resting (R) sites, respectively, are as follows: north: F = 16, R = 2; east: F = 10, R = 4; south: F = 4, R = 2, west: F = 5, R = 0.

values across the 5 points. I recorded aspect as north, east, south, west, and flat at the plot center.

I estimated stem density using the point-center-quarter method (Cottam and Curtis 1956) for all trees ≥ 5 cm in diameter at breast height (dbh). I measured exact distances to all trees except when the closest tree was > 100 m away; then I used 100 m in density estimation. I also recorded the dbh and height of each tree. I collected this data at 5 sampling points per plot (plot center and at the end of each 25-m radial transect).

I multiplied the mean dbh of trees by the number of stems to determine the basal area of trees (m^2/ha), and averaged all tree heights to establish a mean canopy height (m). However, I listed mean canopy height as 0 if the basal area of a site was < 1 m^2/ha to prevent the illusion of a high canopy when no real canopy was present (i.e., an open area with 1 large tree would be represented as having a large mean canopy value). I measured basal area of snags (m^2/ha) ≥ 10 cm dbh using a 10 basal area factor prism at plot center and at the end of 2 randomly chosen radial transects, and used the mean in analyses.

I assessed vertical cover through the use of a 2 m × 0.2 m cover-board checkered with 0.1 m × 0.1 m black and white squares. The percentage of board covered was recorded in all 4 cardinal directions at plot center. Additionally, I used a spherical densitometer to determine canopy cover with readings taken in all 4 cardinal directions at plot center. I repeated vertical cover and canopy cover measurements at the end of 2 randomly chosen radial transects and used the mean values in analyses. For comparative purposes, I recorded these same characteristics at randomly selected sites that were representative of all covertypes present in RMNP. I sampled bear locations within 2 weeks after observation with all sites sampled from May–August.

I tested for differences between foraging and resting locations of black bears for all site-specific variables except aspect using Mann–Whitney *U*-tests (Zar 1999); differences in aspect were assessed with χ^2 analyses (Zar 1999). I used logistic regression (Hosmer and Lemeshow 2000) to model site-specific characteristics between random and known foraging and resting locations using both univariate and multivariate models. All analytical and model selection procedures followed those listed for landscape-level analyses, although I divided stem densities by 100 to facilitate interpretation of odds ratios.

Body condition-habitat relationships

I located and immobilized (see above) collared black bears in dens during early hibernation to assess the nutritional condition attained by bears during the previous year (see Chapter 2). I used bioelectrical impedence analysis (BIA) to assess percent body fat (BF) in bears during den checks. This technique measured the resistance of an electrical current that was passed through the bear and related this resistance measurement to dorsal contour length (excluding tail measurement) and weight to estimate BF (Farley and Robbins 1994, Hilderbrand et al. 1998). For resistance measurements, I placed bears in a sternally recumbent position with hind legs extended backward and front legs extended forward parallel to the length of the body (Gau and Case 1999, 2002). I placed bears on a plastic tarp to eliminate conductivity problems associated with wet ground (Farley and Robbins 1994, Atkinson and Ramsay 1995). I positioned electrodes in a snout to tail configuration with alligator clamps attached to the lips and needle electrodes inserted 3 cm to either side of the base of the tail (Farley and Robbins 1994). Measurements were taken multiple times to verify readings. Additionally, I measured body condition index (BCI) scores for black bears using straight-line body length and weight (Cattet et al. 2002). Derived BCI values are strongly correlated to true body condition ($r = 1.0$, $P < 0.001$;

Cattet et al. 2002) and reflect the combined mass of BF and skeletal muscle of an individual relative to its body size (see Chapter 2 for further detail on BF and BCI methods).

I modeled BCI and BF values of individual black bears as a function of percent home-range composition (i.e., landscape scale) and percent home-range locations (i.e., home-range scale) in covertypes (Table 1) using simple linear regression (Zar 1999) to assess the influence of each covertype on body condition. I performed separate analyses for annual, spring, summer, and autumn home-ranges to assess the influence of each covertype on condition indices both seasonally and annually. Additionally, I included landscape metrics (see Table 2) from annual home-ranges in models to determine any influence of these factors on nutritional condition.

RESULTS

Landscape

Contemporary period.—Most (20 of 24) habitat variables were related to home-range characteristics at the landscape scale (Table 4) when assessing both east and west sides combined. Of the significant variables, Shannon's diversity ($\chi^2 = 36.2$, $P < 0.001$; odds ratio = > 999.9 [95% CI = 108.0–> 999.9]), Shannon's evenness ($\chi^2 = 34.4$, $P < 0.001$; odds ratio = 1.4 [95% CI = 1.2–1.6]), and interspersion and juxtaposition ($\chi^2 = 31.4$, $P < 0.001$; odds ratio = 1.3 [95% CI = 1.2–1.5]) indices were the landscape components most strongly related to black bear home-ranges (Table 4), and collectively indicated a preference for a greater number of evenly distributed patches. Aspen ($\chi^2 = 29.9$, $P < 0.001$; odds ratio = 3.7 [95% CI = 2.1–6.4]) and human-use areas ($\chi^2 = 23.2$, $P < 0.001$; odds ratio = 1.06 [95% CI = 1.03–1.09]) were the covertypes most strongly related to composition of black bear home-ranges in RMNP; positive β's indicated overrepresentation of these variables in black bear home-ranges (Table 4). A

Table 7.4. Logistic regression results relating covertypes and landscape metrics of black bear home-ranges (n = 21) to 100 randomly generated home-ranges throughout Rocky Mountain National Park, Colorado, 2004–2006. Values reported include likelihood ratio (for Model) and Wald (for Parameter) χ^2 statistics (χ^2) and associated P values (P), Schwartz information criterion (SIC) values, maximum rescaled generalized R^2 (R^2), percent concordance (% con), and parameter estimates (β) and associated standard errors (SE). The 5 highest scoring variables are in bold.

	Model					Parameter			
Variable	χ^2	P	SIC	R^2	% con	β	SE	χ^2	P
Herbaceous meadow	8.2	0.004	113.1	0.108	65.5	–0.100	0.042	5.7	0.017
Herbaceous wetland	17.4	<0.001	103.9	0.222	78.9	–0.249	0.084	8.8	0.003
Xeric shrubland	0.0	0.949	121.3	0.000	22.1	–0.005	0.079	0.0	0.949
Mesic shrubland	0.0	0.861	121.2	0.000	51.8	0.016	0.093	0.0	0.860
Aspen	29.9	<0.001	91.4	0.363	85.3	1.305	0.279	21.9	<0.001
Mixed conifer with aspen	10.9	0.001	110.3	0.144	72.8	0.221	0.074	9.0	0.003
Mixed conifer	3.7	0.056	117.6	0.049	62.7	–0.029	0.016	3.4	0.064
Riparian mixed conifer	2.5	0.111	118.7	0.035	69.3	0.191	0.119	2.6	0.107
Krummholz	11.0	0.001	110.3	0.144	68.0	–0.442	0.161	7.6	0.006
Limber pine	16.8	<0.001	104.5	0.215	73.8	0.266	0.073	13.2	<0.001
Lodgepole pine	2.0	0.161	119.3	0.027	67.4	0.018	0.013	2.1	0.152
Ponderosa pine	11.2	0.001	110.1	0.147	80.0	0.088	0.027	11.0	0.001
Douglas fir	13.7	<0.001	107.6	0.178	78.7	0.092	0.025	13.4	<0.001
Dead and down	8.7	0.003	112.6	0.115	58.3	0.538	0.197	7.5	0.006
Rock	17.8	<0.001	103.5	0.227	72.9	–0.182	0.068	7.1	0.008
Non-vegetated surface	9.9	0.002	111.3	0.131	70.6	1.604	0.521	9.5	0.002
Human-use area	23.2	<0.001	98.1	0.289	81.8	0.057	0.014	17.7	<0.001
Patch density	12.1	0.001	109.1	0.159	73.7	0.220	0.067	10.8	0.001
Edge density	15.6	<0.001	105.7	0.201	77.4	0.025	0.007	13.4	<0.001
Total core area index	17.4	<0.001	103.9	0.222	77.9	–0.143	0.039	13.7	<0.001
AWMSI[a]	15.2	<0.001	106.1	0.196	74.4	–1.246	0.387	10.3	0.001
Shannon diversity index	36.2	<0.001	85.1	0.429	86.7	7.935	1.660	22.9	<0.001
Shannon evenness index	34.4	<0.001	86.9	0.411	86.8	0.333	0.074	20.0	<0.001
IJI[b]	31.4	<0.001	89.9	0.379	85.4	0.261	0.059	19.8	<0.001

[a] Area weighted mean shape index.

[b] Interspersion and juxtaposition index.

multivariate model containing limber pine (χ^2 = 5.2, P = 0.023; β = 0.176 [SE = 0.077]; odds ratio = 1.19 [95% CI = 1.03–1.39]), dead and down (χ^2 = 6.6, P = 0.010; β = 0.657 [SE = 0.255]; odds ratio = 1.9 [95% CI = 1.2–3.2]), and Shannon's evenness index (χ^2 = 12.6, $P < 0.001$; β = 0.293 [SE = 0.083]; odds ratio = 1.3 [95% CI = 1.1–1.6]) was the best supported multivariate model of black bear habitat use (χ^2 = 45.8, $P < 0.001$, R^2 = 0.52, con = 90.4%) (Table 5). This model indicated that black bear home-ranges included greater proportions of limber pine and dead and down areas and greater evenness in patch distribution.

During the contemporary period, 19 of 24 variables were associated with home-range composition east of the continental divide (Table 6). Among covertypes, herbaceous meadows (χ^2 = 14.6, $P < 0.001$; odds ratio = 0.87 [95% CI = 0.80–0.96]) and rocky areas (χ^2 = 14.3, $P <$ 0.001; odds ratio = 0.82 [95% CI = 0.70–0.96]) had the strongest negative associations, while aspen (χ^2 = 15.2, $P < 0.001$; odds ratio = 2.6 [95% CI = 1.5–4.6]) showed the strongest positive relationship (Table 6). Shannon's evenness (χ^2 = 25.8, $P < 0.001$; odds ratio = 1.5 [95% CI = 1.2–1.8]), Shannon's diversity (χ^2 = 18.2, $P < 0.001$; odds ratio > 999.9 [95% CI = 21.9–> 999.9]), and interspersion and juxtaposition indices (χ^2 = 21.3, $P < 0.001$; odds ratio = 1.3 [95% CI = 1.1–1.5]) were all positively associated with black bear home-range composition, indicating a preference for more diverse and evenly distributed patches (Table 6). The best supported multivariate model (χ^2 = 37.0, $P < 0.001$, R^2 = 0.59, con = 90.3%) included Shannon's evenness index (χ^2 = 11.4, $P < 0.001$; β = 0.486 [SE = 0.144]; odds ratio = 1.6 [95% CI = 1.2–2.2]), Douglas fir (χ^2 = 6.6, P = 0.010; β = –0.201 [SE = 0.078]; odds ratio = 0.82 [95% CI = 0.70–0.95]), and krummholz (χ^2 = 6.4, P = 0.011; β = –0.763 [SE = 0.301]; odds ratio = 0.5 [95% CI = 0.3–0.8]), with black bears selecting home-ranges with greater evenness of habitat patches, but less krummholz and Douglas fir (Table 7). Collectively, aspen, interspersion and juxtaposition,

Table 7.5. Summary of selected black bear habitat-use models at the landscape scale for Rocky Mountain National Park, Colorado, during the contemporary period (2004–2006). Models were constructed collectively for both the eastern and western sides of the continental divide. Values reported include likelihood ratio χ^2 statistics (χ^2) and associated *P* values (*P*), Schwartz information criterion (SIC) values, the difference in SIC when compared to the top models (ΔSIC), percent concordance (% con), maximum rescaled generalized R^2 (R^2), and the summation of the rank scores (Σ rank) when comparing models through ΔSIC, R^2, and % con. The preferred model is in bold.

Model[a]	χ^2	*P*	SIC	ΔSIC	R^2	% con	Σ rank
Limp, dd, sei	**45.8**	**<0.001**	**85.08**	**0.84**	**0.523**	**90.4**	**4**
Limp, dd, k, sei	49.0	<0.001	86.67	2.43	0.552	90.1	7
Limp, mcwa, sei	44.4	<0.001	86.45	2.21	0.510	89.7	8
Dd, k, sei	44.2	<0.001	86.66	2.42	0.508	89.4	11

[a] Variable notation: limp = limber pine, dd = dead and down, sei = Shannon's evenness index, k = krummholz, and mcwa = mixed conifer with aspen.

Table 7.6. Logistic regression results relating covertypes and landscape metrics of black bear home-ranges (n = 20) east of the continental divide to 50 randomly generated home-ranges in the eastern portion of Rocky Mountain National Park, Colorado, 2004–2006. Values reported include likelihood ratio (for Model) and Wald (for Parameter) χ^2 statistics (χ^2) and associated P values (P), Schwartz information criterion (SIC) values, maximum rescaled generalized R^2 (R^2), percent concordance (% con), and parameter estimates (β) and associated standard errors (SE). The 6 highest scoring variables are in bold.

	Model					Parameter			
Variable	χ^2	P	SIC	R^2	% con	β	SE	χ^2	P
Herbaceous meadow	14.6	<0.001	77.7	0.270	73.5	–0.134	0.046	8.7	0.003
Herbaceous wetland	5.5	0.019	86.8	0.108	66.6	–0.136	0.075	3.3	0.069
Xeric shrubland	0.4	0.543	91.9	0.008	49.9	–0.057	0.097	0.3	0.557
Mesic shrubland	4.2	0.041	88.1	0.083	66.4	0.316	0.158	4.0	0.046
Aspen	15.2	<0.001	77.0	0.281	78.7	0.970	0.281	11.9	0.001
Mixed conifer with aspen	4.1	0.044	88.2	0.081	64.7	0.128	0.067	3.6	0.057
Mixed conifer	0.3	0.611	92.0	0.005	52.3	–0.008	0.017	0.3	0.613
Riparian mixed conifer	2.0	0.153	90.2	0.041	65.2	0.263	0.185	2.0	0.155
Krummholz	13.0	<0.001	79.2	0.243	67.8	–0.429	0.143	9.0	0.003
Limber pine	5.5	0.019	86.7	0.109	62.8	0.161	0.073	4.9	0.027
Lodgepole pine	13.0	<0.001	79.2	0.243	77.9	0.088	0.027	10.8	0.001
Ponderosa pine	1.5	0.221	90.8	0.030	69.2	0.030	0.024	1.5	0.218
Douglas fir	2.9	0.086	89.3	0.059	64.5	0.045	0.026	2.9	0.088
Dead and down	3.8	0.053	88.5	0.075	54.4	0.349	0.189	3.4	0.064
Rock	14.3	<0.001	77.9	0.266	73.1	–0.201	0.083	5.8	0.016
Non-vegetated surface	3.0	0.081	89.2	0.061	66.4	0.814	0.474	2.9	0.086
Human-use area	10.3	0.001	81.9	0.197	73.5	0.040	0.014	8.6	0.004
Patch density	1.5	0.220	90.8	0.031	86.3	0.093	0.077	1.5	0.228
Edge density	3.6	0.058	88.6	0.072	64.6	0.013	0.007	3.4	0.065
Total core area index	8.7	0.003	83.6	0.167	71.2	–0.103	0.038	7.5	0.006
AWMSI[a]	12.2	0.001	80.0	0.230	75.5	–1.311	0.487	7.3	0.007
Shannon diversity index	18.2	<0.001	74.1	0.328	80.0	7.087	2.041	12.1	0.001
Shannon evenness index	25.8	<0.001	66.5	0.442	85.4	0.378	0.097	15.1	<0.001
IJI[b]	21.3	<0.001	71.0	0.376	82.5	0.267	0.071	14.2	<0.001

[a] Area weighted mean shape index.

[b] Interspersion and juxtaposition index.

Table 7.7. Summary of selected black bear habitat-use models at the landscape scale for the eastern side of the continental divide in Rocky Mountain National Park, Colorado, during the contemporary period (2004–2006). Values reported include likelihood ratio χ^2 statistics (χ^2) and associated *P* values (*P*), Schwartz information criterion (SIC) values, the difference in SIC when compared to the top models (ΔSIC), percent concordance (% con), maximum rescaled generalized R^2 (R^2), and the summation of the rank scores (Σ rank) when comparing models through ΔSIC, R^2, and % con. The preferred model is in bold.

Model[a]	χ^2	*P*	SIC	ΔSIC	R^2	% con	Σ rank
Mdf, k, sei	**37.0**	**<0.001**	**63.80**	**0.00**	**0.588**	**90.3**	**3**
Limp, dd, sei	33.8	<0.001	66.96	3.16	0.549	89.7	6
Hm, mdf, sei	33.1	<0.001	67.61	3.81	0.541	88.3	9

[a] Variable notation: mdf = montane Douglas fir, k = krummholz, sei = Shannon’s evenness index, limp = limber pine, dd = dead and down, and hm = herbaceous meadow.

and Shannon's diversity and evenness indices were associated with black bear home-ranges more frequently than any other variables, and in all cases were positively associated with black bear home-ranges in RMNP during the contemporary period (Tables 4–7).

Occupancy models.—Only 1 model fit the model selection criteria and indicated selection for western RMNP ($\chi^2 = 12.3$, $P < 0.001$; $\beta = -3.902$ [SE = 1.115]; odds ratio = 0.020 [90% CI = 0.003–0.130]); for greater amounts of non-vegetated surfaces ($\chi^2 = 8.1$, $P = 0.004$; $\beta = 1.155$ [SE = 0.406]; odds ratio = 3.2 [90% CI = 1.6–6.3]), krummholz ($\chi^2 = 3.1$, $P = 0.080$; $\beta = 0.291$ [SE = 0.166]; odds ratio = 1.34 [90% CI = 1.01–1.77]), and limber pine stands ($\chi^2 = 9.4$, $P = 0.002$; $\beta = 0.306$ [SE = 0.100]; odds ratio = 1.4 [90% CI = 1.1–1.6]); and for less area associated with mesic shrublands ($\chi^2 = 3.3$, $P = 0.070$; $\beta = -0.321$ [SE = 0.177]; odds ratio = 0.73 [90% CI = 0.54–0.98]) by black bears in late summer–autumn.

Historic period.—For east and west sides combined, 19 of 24 habitat variables were related to black bear home-range characteristics at the landscape scale (Table 8). Area weighted mean shape index (AWMSI) exhibited the strongest relationship among landscape metrics ($\chi^2 = 24.0$, $P < 0.001$; odds ratio = 0.14 [95% CI = 0.05–0.40]), indicating a preference for less complex shapes of habitat patches (i.e., less perimeter per area for each patch). Home-range composition was strongly negatively related to rock ($\chi^2 = 21.9$, $P < 0.001$; odds ratio = 0.7 [95% CI = 0.6–0.9]), krummholz ($\chi^2 = 19.7$, $P < 0.001$; odds ratio = 0.4 [95% CI = 0.2–0.8]), and herbaceous meadow covertypes ($\chi^2 = 17.4$, $P < 0.001$; odds ratio = 0.8 [95% CI = 0.7–0.9]), while human-use areas ($\chi^2 = 17.4$, $P < 0.001$; odds ratio = 1.06 [95% CI = 1.03–1.09]) exhibited a positive relationship (Table 8). The best multivariate model ($\chi^2 = 41.6$, $P < 0.001$, $R^2 = 0.55$, con = 92.1%) included limber pine ($\chi^2 = 4.4$, $P = 0.035$; $\beta = 0.257$ [SE = 0.122]; odds ratio = 1.29 [95% CI = 1.02–1.64]), Douglas fir ($\chi^2 = 3.5$, $P = 0.062$; $\beta = -0.094$ [SE = 0.050]; odds

Table 7.8. Logistic regression results relating covertypes and landscape metrics of black bear home-ranges (n = 16) to 100 randomly generated home-ranges throughout Rocky Mountain National Park, Colorado, 1984–1991. Values reported include likelihood ratio (for Model) and Wald (for Parameter) χ^2 statistics (χ^2) and associated P values (P), Schwartz information criterion (SIC) values, maximum rescaled generalized R^2 (R^2), percent concordance (% con), and parameter estimates (β) and associated standard errors (SE). The 5 highest scoring variables are in bold.

	Model					Parameter			
Variable	χ^2	P	SIC	R^2	% con	β	SE	χ^2	P
Herbaceous meadow	17.4	<0.001	85.2	0.253	81.6	–0.235	0.086	7.6	0.006
Herbaceous wetland	14.5	<0.001	88.1	0.213	76.1	–0.265	0.098	7.4	0.007
Xeric shrubland	8.9	0.003	93.7	0.134	64.0	–0.917	0.560	2.7	0.101
Mesic shrubland	2.8	0.093	99.8	0.044	65.9	0.138	0.079	3.0	0.081
Aspen	14.3	<0.001	88.2	0.211	84.6	1.019	0.279	13.4	<0.001
Mixed conifer with aspen	4.7	0.030	97.9	0.072	71.8	0.155	0.071	4.8	0.028
Mixed conifer	0.0	0.943	102.6	0.000	36.4	0.001	0.017	0.0	0.943
Riparian mixed conifer	5.6	0.018	97.0	0.086	70.9	0.278	0.118	5.6	0.019
Krummholz	19.7	<0.001	82.9	0.283	76.3	–0.996	0.366	7.4	0.007
Limber pine	8.6	0.003	93.9	0.130	59.8	0.237	0.079	9.0	0.003
Lodgepole pine	8.8	0.003	93.8	0.133	79.4	0.040	0.014	8.6	0.003
Ponderosa pine	0.0	0.892	102.6	0.000	37.9	0.005	0.038	0.0	0.891
Douglas fir	3.6	0.059	99.0	0.055	70.4	0.055	0.028	3.9	0.048
Dead and down	0.8	0.358	101.7	0.013	36.6	0.260	0.266	1.0	0.328
Rock	21.9	<0.001	80.7	0.311	81.0	–0.337	0.126	7.1	0.008
Non-vegetated surface	13.2	<0.001	89.3	0.195	73.6	1.880	0.627	9.0	0.003
Human-use area	17.4	<0.001	85.2	0.252	83.5	0.055	0.015	13.8	<0.001
Patch density	2.1	0.145	100.5	0.033	58.9	0.101	0.069	2.1	0.144
Edge density	1.9	0.165	100.7	0.030	61.1	0.010	0.007	2.0	0.162
Total core area index	4.1	0.042	98.4	0.064	66.6	–0.075	0.038	3.8	0.050
AWMSI[a]	24.0	<0.001	78.5	0.339	84.8	–1.969	0.541	13.3	<0.001
Shannon diversity index	8.8	0.003	93.7	0.133	70.0	3.882	1.342	8.4	0.004
Shannon evenness index	3.8	0.050	98.8	0.059	62.4	0.099	0.052	3.6	0.057
IJI[b]	4.2	0.040	98.3	0.065	63.3	0.089	0.044	4.0	0.044

[a] Area weighted mean shape index.

[b] Interspersion and juxtaposition index.

ratio = 0.911 [95% CI = 0.825–1.005]), krummholz ($\chi^2 = 6.9$, $P = 0.008$; $\beta = -1.089$ [SE = 0.414]; odds ratio = 0.3 [95% CI = 0.2–0.8]), and AWMSI ($\chi^2 = 7.9$, $P = 0.005$; $\beta = -1.478$ [SE = 0.527]; odds ratio = 0.2 [95% CI = 0.1–0.6]) and indicated a preference for sites with less complex shapes of habitat patches, more limber pine, but less krummholz (Table 9). The influence of Douglas fir was weak given odds ratios that overlapped 1. An equally ranked model included a positive association with riparian mixed conifer along with the previously mentioned variables ($\chi^2 = 45.8$, $P < 0.001$, $R^2 = 0.59$, con = 94.2%), but was not further considered given the more parsimonious nature of the selected model.

During the historic period, 18 of 24 habitat variables were associated with home-range composition for black bears east of the continental divide (Table 10). Among landscape metrics, AWMSI ($\chi^2 = 41.0$, $P < 0.001$; odds ratio < 0.001 [95% CI = < 0.001–0.087]) showed the strongest relationship, with black bears selecting home-ranges in locations with habitat patches of less complexity (Table 10). Additionally, home-ranges with lodgepole pine ($\chi^2 = 14.6$, $P < 0.001$; odds ratio = 1.12 [95% CI = 1.05–1.20]) were preferred, while herbaceous meadows ($\chi^2 = 13.6$, $P < 0.001$; odds ratio = 0.83 [95% CI = 0.70–0.97]), krummholz ($\chi^2 = 12.7$, $P < 0.001$; odds ratio = 0.5 [95% CI = 0.3–0.9]), and rock ($\chi^2 = 12.4$, $P < 0.001$; odds ratio = 0.72 [95% CI = 0.54–0.98]) covertypes were selected against (Table 10). The best multivariate model ($\chi^2 = 45.2$, $P < 0.001$, $R^2 = 0.86$, con = 95.1%) included AWMSI ($\chi^2 = 6.5$, $P = 0.011$; $\beta = -10.758$ [SE = 4.224]; odds ratio = < 0.001 [95% CI = < 0.001–0.084]) and limber pine ($\chi^2 = 2.8$, $P = 0.096$; $\beta = 0.450$ [SE = 0.270]; odds ratio = 1.6 [95% CI = 0.9–2.7]) and indicated a preference for stands with habitat patches of less complexity (Table 11); the presence of limber pine in the model was uninformative given odds ratios that included 1.

Table 7.9. Summary of selected black bear habitat-use models at the landscape scale for Rocky Mountain National Park, Colorado, during the historic period (1984–1991). Models were constructed collectively for both the eastern and western sides of the continental divide. Values reported include likelihood ratio χ^2 statistics (χ^2) and associated P values (P), Schwartz information criterion (SIC) values, the difference in SIC when compared to the top models (ΔSIC), percent concordance (% con), maximum rescaled generalized R^2 (R^2), and the summation of the rank scores (Σ rank) when comparing models through ΔSIC, R^2, and % con. The preferred model is in bold.

Model[a]	χ^2	P	SIC	ΔSIC	R^2	% con	Σ rank
Limp, k, mdf, awmsi	**41.6**	**<0.001**	**75.23**	**3.19**	**0.546**	**92.1**	**5**
Limp, k, mdf, rmc, humu	45.8	<0.001	75.80	3.76	0.591	94.2	5
Rmc, awmsi, nv, hm	41.4	<0.001	75.43	3.39	0.544	91.2	8

[a] Variable notation: limp = limber pine, k = krummholz, mdf = montane Douglas fir, awmsi = area weighted mean shape index, rmc = riparian mixed conifer, humu = human-use areas, nv = non-vegetated surfaces, and hm = herbaceous meadows.

Table 7.10. Logistic regression results relating covertypes and landscape metrics of black bear home-ranges (n = 11) east of the continental divide to 50 randomly generated home-ranges in the eastern portion of Rocky Mountain National Park, Colorado, 1984–1991. Values reported include likelihood ratio (for Model) and Wald (for Parameter) χ^2 statistics (χ^2) and associated P values (P), Schwartz information criterion (SIC) values, maximum rescaled generalized R^2 (R^2), percent concordance (% con), and parameter estimates (β) and associated standard errors (SE). The 5 highest scoring variables are in bold.

	Model					Parameter			
Variable	χ^2	P	SIC	R^2	% con	β	SE	χ^2	P
Herbaceous meadow	13.6	<0.001	52.2	0.327	82.4	–0.193	0.083	5.4	0.020
Herbaceous wetland	9.8	0.002	56.0	0.244	75.1	–0.441	0.230	3.7	0.055
Xeric shrubland	9.5	0.002	56.3	0.236	70.9	–1.091	0.621	3.1	0.079
Mesic shrubland	6.1	0.014	59.7	0.155	68.7	0.366	0.190	3.7	0.055
Aspen	10.4	0.001	55.4	0.258	82.0	1.020	0.345	8.7	0.003
Mixed conifer with aspen	2.1	0.144	63.7	0.056	63.8	0.108	0.072	2.2	0.135
Mixed conifer	0.4	0.522	65.4	0.011	58.0	0.013	0.020	0.4	0.522
Riparian mixed conifer	9.4	0.002	56.4	0.233	77.1	0.546	0.194	7.9	0.005
Krummholz	12.7	<0.001	53.1	0.308	72.2	–0.657	0.279	5.5	0.019
Limber pine	6.1	0.013	59.6	0.157	65.1	0.253	0.106	5.7	0.017
Lodgepole pine	14.6	<0.001	51.2	0.349	85.8	0.114	0.035	10.4	0.001
Ponderosa pine	0.6	0.444	65.2	0.016	32.0	–0.028	0.040	0.5	0.477
Douglas fir	1.2	0.265	64.5	0.033	70.2	0.036	0.032	1.3	0.259
Dead and down	0.1	0.725	65.7	0.003	35.1	0.105	0.290	0.1	0.718
Rock	12.4	<0.001	53.4	0.302	78.2	–0.325	0.154	4.5	0.035
Non-vegetated surface	4.2	0.041	61.6	0.108	64.4	0.618	0.448	1.9	0.167
Human-use area	5.0	0.026	60.8	0.128	72.5	0.033	0.016	4.5	0.035
Patch density	0.2	0.638	65.6	0.006	52.2	0.043	0.093	0.2	0.640
Edge density	0.3	0.589	65.5	0.008	57.6	0.005	0.009	0.3	0.589
Total core area index	2.4	0.125	63.4	0.062	64.4	–0.065	0.043	2.2	0.135
AWMSI[a]	41.0	<0.001	24.7	0.802	97.5	–9.235	3.464	7.1	0.008
Shannon diversity index	6.9	0.009	58.9	0.174	72.2	4.936	2.104	5.5	0.019
Shannon evenness index	10.5	0.001	55.3	0.258	79.1	0.267	0.095	7.9	0.005
IJI[b]	9.7	0.002	56.1	0.240	79.1	0.206	0.074	7.7	0.006

[a] Area weighted mean shape index.

[b] Interspersion and juxtaposition index.

Table 7.11. Summary of selected black bear habitat-use models at the landscape scale for the eastern side of the continental divide in Rocky Mountain National Park, Colorado, during the historic period (1984–1991). Values reported include likelihood ratio χ^2 statistics (χ^2) and associated *P* values (*P*), Schwartz information criterion (SIC) values, the difference in SIC when compared to the top models (ΔSIC), percent concordance (% con), maximum rescaled generalized R^2 (R^2), and the summation of the rank scores (Σ rank) when comparing models through ΔSIC, R^2, and % con. The preferred model is in bold.

Model[a]	χ^2	*P*	SIC	ΔSIC	R^2	% con	Σ rank
Awmsi, limp	**45.2**	**<0.001**	**24.69**	**0.00**	**0.857**	**95.1**	**4**
Awmsi	41.0	<0.001	24.74	0.05	0.802	97.5	5

[a] Variable notation: awmsi = area weighted mean shape index and limp = limber pine.

West of the continental divide, fewer variables (12 of 24) were associated with black bear home-ranges (Table 12). No landscape metrics were strongly associated with black bear home-ranges, with only Shannon's evenness (χ^2 = 3.8, P = 0.053; odds ratio = 0.81 [95% CI = 0.64–1.03]) and interspersion and juxtaposition (χ^2 = 3.0, P = 0.084; odds ratio = 0.85 [95% CI = 0.70–1.04]) indices exhibiting a significant relationship (Table 12); odds ratios including 1 indicated the weak nature of these associations. Among covertypes, human-use areas (χ^2 = 16.6, P < 0.001; odds ratio = 1.21 [95% CI = 1.03–1.41]) and non-vegetated surfaces (χ^2 = 11.8, P = 0.001; odds ratio = 90.1 [95% CI = 4.0–> 999.9]) were overrepresented in home-ranges. Only 1 multivariate model (χ^2 = 16.3, P < 0.001, R^2 = 0.56, con = 95.6%) fit my selection criteria and included non-vegetated surfaces (χ^2 = 5.6, P = 0.018; β = 4.296 [SE = 1.820]; odds ratio = 73.4 [95% CI = 2.1–> 999.9]) and mixed conifer with aspen (χ^2 = 4.0, P = 0.045; β = 2.016 [SE = 1.005]; odds ratio = 7.51 [95% CI = 1.05–53.76]); black bears selected home-ranges with more non-vegetated surfaces (i.e., asphalt, dirt roads, etc.) and mixed conifer with aspen patches (Table 13). However, the univariate model for human-use areas (χ^2 = 5.2, P = 0.022; β = 0.186 [SE = 0.082]; odds ratio = 1.21 [95% CI = 1.03–1.41]) had lower SIC and higher R^2 values (Table 13) than the multivariate model and was better supported than any multivariate model. Collectively, herbaceous meadows (negative association), rock (negative), krummholz (negative), human-use areas (positive association), non-vegetated surfaces (positive), and AWMSI (negative) were associated with black bear home-ranges more frequently than other variables for the historical period in RMNP (Tables 8–13).

Home-range

Annually, herbaceous meadows, xeric shrublands, and krummholz were always avoided by black bears (Table 14). Other covertypes varied depending on year, though limber pine and

Table 7.12. Logistic regression results relating covertypes and landscape metrics of black bear home-ranges (n = 5) west of the continental divide to 50 randomly generated home-ranges in the western portion of Rocky Mountain National Park, Colorado, 1984–1991. Values reported include likelihood ratio (for Model) and Wald (for Parameter) χ^2 statistics (χ^2) and associated P values (P), Schwartz information criterion (SIC) values, maximum rescaled generalized R^2 (R^2), percent concordance (% con), and parameter estimates (β) and associated standard errors (SE). The 2 highest scoring variables are in bold.

	Model					Parameter			
Variable	χ^2	P	SIC	R^2	% con	β	SE	χ^2	P
Herbaceous meadow	12.1	0.001	29.4	0.434	89.6	–0.724	0.370	3.8	0.050
Herbaceous wetland	3.5	0.061	38.0	0.135	73.6	–0.180	0.123	2.1	0.144
Xeric shrubland	3.2	0.074	38.3	0.124	63.6	–2.329	2.409	0.9	0.334
Mesic shrubland	0.4	0.537	41.1	0.015	64.8	0.086	0.135	0.4	0.524
Aspen	2.8	0.096	38.8	0.108	76.0	2.709	1.644	2.7	0.099
Mixed conifer with aspen	7.9	0.005	33.6	0.293	90.8	2.229	0.860	6.7	0.010
Mixed conifer	0.0	0.845	41.5	0.002	47.2	0.007	0.034	0.0	0.845
Riparian mixed conifer	0.0	0.945	41.5	0.000	22.0	–0.015	0.224	0.0	0.946
Krummholz	10.7	0.001	30.8	0.388	83.6	–2.668	1.652	2.6	0.106
Limber pine	0.0	0.859	41.5	0.001	25.2	–0.317	1.848	0.0	0.864
Lodgepole pine	6.4	0.012	35.2	0.240	85.6	0.055	0.024	5.2	0.023
Ponderosa pine	0.0	0.878	41.5	0.001	16.0	–0.584	3.974	0.0	0.883
Douglas fir	0.0	0.911	41.5	0.001	22.0	–0.105	0.968	0.0	0.914
Dead and down	1.5	0.227	40.1	0.013	54.8	2.233	1.734	1.7	0.198
Rock	10.9	0.001	30.7	0.393	86.4	–0.634	0.426	2.2	0.137
Non-vegetated surface	11.8	0.001	29.7	0.424	92.0	4.501	1.584	8.1	0.005
Human-use area	16.6	<0.001	25.0	0.570	92.8	0.186	0.082	5.2	0.022
Patch density	0.0	0.985	41.5	0.000	24.4	0.004	0.192	0.0	0.985
Edge density	0.1	0.820	41.5	0.002	54.0	–0.004	0.019	0.1	0.820
Total core area index	0.1	0.720	41.4	0.005	51.6	–0.026	0.075	0.1	0.726
AWMSI[a]	0.8	0.380	40.7	0.031	62.0	–0.480	0.569	0.7	0.399
Shannon diversity index	0.2	0.662	41.3	0.008	55.2	2.007	4.651	0.2	0.666
Shannon evenness index	3.8	0.053	37.8	0.144	78.8	–0.211	0.121	3.1	0.081
IJI[b]	3.0	0.084	38.5	0.116	76.4	–0.160	0.100	2.6	0.107

[a] Area weighted mean shape index.

[b] Interspersion and juxtaposition index.

Table 7.13. Summary of selected black bear habitat-use models at the landscape scale for the western side of the continental divide in Rocky Mountain National Park, Colorado, during the historic period (1984–1991). Values reported include likelihood ratio χ^2 statistics (χ^2) and associated *P* values (*P*), Schwartz information criterion (SIC) values, the difference in SIC when compared to the top models (ΔSIC), percent concordance (% con), maximum rescaled generalized R^2 (R^2), and the summation of the rank scores (Σ rank) when comparing models through ΔSIC, R^2, and % con. The preferred model is in bold.

Model[a]	χ^2	*P*	SIC	ΔSIC	R^2	% con	Σ rank
Humu	**16.6**	**<0.001**	**24.95**	**0.99**	**0.570**	**92.8**	**4**
Nv, mcwa	16.3	<0.001	29.26	5.30	0.561	95.6	5

[a] Variable notation: humu = human-use areas, nv = non-vegetated surfaces, and mcwa = mixed conifer with aspen.

Table 7.14. Mean differences by habitat type between proportion of annual locations within habitat types and proportion of habitat types available within annual home-ranges (significant differences in bold) for black bears in Rocky Mountain National Park, Colorado. Selection ratios (SR = percent use/percent availability) are listed for mean differences that were significant.

	2004		2005		2006		Combined	
Habitat[a]	Mean	SR	Mean	SR	Mean	SR	Mean	SR
HM	**–3.22**	**0.28**	**–5.07**	**0.13**	**–5.58**	**0.10**	**–4.83**	**0.15**
HW	**–1.98**	**0.00**	0.37		**–1.34**	**0.00**	–0.69	
XS	**–2.01**	**0.00**	**–2.05**	**0.10**	**–1.65**	**0.00**	**–1.89**	**0.05**
MS	**–4.23**	**0.00**	0.01		0.95		–0.49	
ROCK	–0.03		**–2.48**	**0.00**	0.32		–1.05	
DD	0.81		–0.38		**14.29**	**8.60**	3.21	
K	**–0.65**	**0.00**	**–1.80**	**0.00**	**–1.40**	**0.00**	**–1.43**	**0.00**
LIMP	–1.54		**–2.95**	**0.49**	–1.52		**–2.29**	**0.57**
LP	–0.72		**7.59**	**1.33**	–1.01		3.23	
PP	2.57		–1.20		–5.27		–1.50	
MDF	–2.67		–0.60		4.39		0.60	
RMC	4.41		**–1.91**	**0.48**	**4.89**	**3.19**	1.56	
MC	9.90		3.11		–1.47		3.33	
MCWA	–2.64		**3.37**	**1.89**	**–0.80**	**0.33**	0.68	
ASP	0.43		3.82		1.06		**2.25**	**2.41**
NV	**–0.52**	**0.00**	–0.24		0.12		–0.20	
HUMU	4.06		7.66		–2.11		3.80	

[a] Habitat abbreviations are as follows: HM = herbaceous meadows, HW = herbaceous wetlands, XS = xeric shrublands, MS = mesic shrublands, ROCK = rocky areas, DD = dead and down, K = krummholz, LIMP = limber pine, LP = lodgepole pine, PP = Ponderosa pine, MDF = montane Douglas fir, RMC = riparian mixed conifer, MC = mixed conifer, MCWA = mixed conifer with aspen, ASP = aspen, NV = non-vegetated surfaces, HUMU = human-use areas.

herbaceous meadows were also typically avoided. Generally, results were most dissimilar in 2005, perhaps given the relatively hot, dry growing season (April–October) that year (precipitation [cm]: 2005 = 31.1, 2004 and 2006 = 43.4; $\bar{x}$ maximum temperature [ºC]: 2005 = 20.1, 2004 and 2006 = 18.5). Collectively, aspen yielded the strongest positive association with black bear occurrence (Table 14).

I obtained sufficient locations for only 2 years during the spring season, with herbaceous meadows and wetlands, xeric shrublands, rocky areas, limber pine, and krummholz typically avoided (Table 15). Lodgepole pine showed the strongest positive association. Additionally, human-use areas were preferred in spring 2005 (Table 15), which may also have been related to the hotter, drier climate that year. During summer, herbaceous wetlands, xeric shrublands, rocky and dead and down areas, limber pine, krummholz, and non-vegetated surfaces were typically avoided, while mixed conifer was most consistently preferred (Table 16). Herbaceous meadows and wetlands, xeric and mesic shrublands, rocky and dead and down areas, non-vegetated surfaces, and human-use areas were typically avoided during autumn (Table 17). No consistent positive relationship was noted for any covertype during autumn, though mixed conifer with aspen was selected for during 2005, while montane Douglas fir and riparian mixed conifer was preferred in 2003 (Table 17). Collectively, among all annual and seasonal analyses, herbaceous meadows and wetlands, xeric shrublands, krummholz, and limber pine showed the strongest relationships to black bear use of home-ranges, and were all consistently avoided. Black bears in RMNP were never located in herbaceous meadows, herbaceous wetlands, and krummholz, and were located in xeric shrublands only during the summer.

I had sufficient locations of 11 black bears historically and 8 black bears contemporarily to conduct MaxEnt modeling procedures. For the historic period, I did not observe a consistent

Table 7.15. Mean differences by habitat type between proportion of spring locations within habitat types and proportion of habitat types available within spring home-ranges (significant differences in bold) for black bears in Rocky Mountain National Park, Colorado. Selection ratios (SR = percent use/percent availability) are listed for mean differences that were significant.

	2005		2006		Combined	
Habitat[a]	Mean	SR	Mean	SR	Mean	SR
HM	**–4.68**	**0.00**	–3.82		**–4.29**	**0.26**
HW	**–1.31**	**0.00**	**–2.06**	**0.00**	**–1.66**	**0.00**
XS	**–1.23**	**0.00**	**–0.97**	**0.00**	**–1.24**	**0.00**
MS	2.39		1.40		0.90	
ROCK	**–2.25**	**0.00**	**–1.88**	**0.00**	–1.21	
DD	1.05		2.79		1.73	
K	**–1.75**	**0.00**	**–1.80**	**0.00**	**–1.78**	**0.00**
LIMP	**–9.71**	**0.00**	–2.06		**–6.12**	**0.09**
LP	6.64		**14.15**	**1.74**	**8.14**	**1.51**
PP	1.51		**–5.52**	**0.00**	–0.64	
MDF	1.46		**–4.10**	**0.35**	–1.11	
RMC	–1.42		2.33		–0.09	
MC	4.90		–0.59		4.69	
MCWA	0.59		–0.75		0.04	
ASP	1.92		3.39		2.14	
NV	1.48		**–0.69**	**0.00**	0.28	
HUMU	**27.78**	**1.56**	–8.43		9.52	

[a] Habitat abbreviations are as follows: HM = herbaceous meadows, HW = herbaceous wetlands, XS = xeric shrublands, MS = mesic shrublands, ROCK = rocky areas, DD = dead and down, K = krummholz, LIMP = limber pine, LP = lodgepole pine, PP = Ponderosa pine, MDF = montane Douglas fir, RMC = riparian mixed conifer, MC = mixed conifer, MCWA = mixed conifer with aspen, ASP = aspen, NV = non-vegetated surfaces, HUMU = human-use areas.

Table 7.16. Mean differences by habitat type between proportion of summer locations within habitat types and proportion of habitat types available within summer home-ranges (significant differences in bold) for black bears in Rocky Mountain National Park, Colorado. Selection ratios (SR = percent use/percent availability) are listed for mean differences that were significant.

	2004		2005		2006		Combined	
Habitat[a]	Mean	SR	Mean	SR	Mean	SR	Mean	SR
HM	–3.09		**–5.67**	**3.26**	0.74		–2.74	
HW	**–5.13**	**0.00**	–0.33		**–0.67**	**0.00**	**–1.72**	**0.46**
XS	**–1.37**	**0.00**	**–1.38**	**0.17**	**–2.68**	**0.00**	**–2.46**	**0.06**
MS	–0.11		0.39		–0.57		0.13	
ROCK	**–4.91**	**0.00**	**–3.46**	**0.00**	0.84		**–2.42**	**0.30**
DD	**–0.67**	**0.00**	**–1.77**	**0.00**	13.13		3.04	
K	**–2.34**	**0.00**	**–2.96**	**0.00**	**–0.52**	**0.00**	**–1.87**	**0.00**
LIMP	**–8.10**	**0.00**	**–4.77**	**0.44**	–2.11		**–4.51**	**0.39**
LP	–3.51		4.92		–6.03		–1.55	
PP	4.70		1.77		–2.59		0.12	
MDF	3.10		–3.02		0.87		1.21	
RMC	–0.80		–1.85		**6.68**	**2.93**	1.80	
MC	18.51		**6.12**	**1.60**	1.25		**8.96**	**3.28**
MCWA	3.60		1.19		–3.78		0.54	
ASP	**–2.92**	**0.00**	**8.87**	**6.36**	–1.35		1.88	
NV	**–1.26**	**0.00**	**–0.57**	**0.00**	0.13		**–0.74**	**0.13**
HUMU	5.93		7.87		–9.44		2.00	

[a] Habitat abbreviations are as follows: HM = herbaceous meadows, HW = herbaceous wetlands, XS = xeric shrublands, MS = mesic shrublands, ROCK = rocky areas, DD = dead and down, K = krummholz, LIMP = limber pine, LP = lodgepole pine, PP = Ponderosa pine, MDF = montane Douglas fir, RMC = riparian mixed conifer, MC = mixed conifer, MCWA = mixed conifer with aspen, ASP = aspen, NV = non-vegetated surfaces, HUMU = human-use areas.

Table 7.17. Mean differences by habitat type between proportion of autumn locations within habitat types and proportion of habitat types available within autumn home-ranges (significant differences in bold) for black bears in Rocky Mountain National Park, Colorado. Selection ratios (SR = percent use/percent availability) are listed for mean differences that were significant.

	2003		2004		2005		Combined	
Habitat[a]	Mean	SR	Mean	SR	Mean	SR	Mean	SR
HM	**–5.32**	**0.00**	**–3.01**	**0.00**	**–3.43**	**0.00**	**–4.09**	**0.00**
HW	**–1.88**	**0.00**	**–0.91**	**0.00**	**–1.06**	**0.00**	**–1.28**	**0.00**
XS	**–3.16**	**0.00**	**–1.92**	**0.00**	–2.02		**–2.35**	**0.22**
MS	–0.81		**–2.92**	**0.00**	**–1.88**	**0.00**	–1.62	
ROCK	**–1.76**	**0.00**	0.98		**–2.40**	**0.00**	–1.15	
DD	**–1.75**	**0.00**	–2.84		**–1.06**	**0.00**	**–1.69**	**0.14**
K	4.01		**–1.77**	**0.00**	**–0.52**	**0.00**	0.35	
LIMP	–3.52		6.38		0.78		1.16	
LP	3.89		3.16		–6.33		0.39	
PP	5.09		–1.43		–1.27		0.72	
MDF	**9.83**	**2.74**	–2.01		1.50		3.59	
RMC	**6.71**	**5.28**	0.61		**–2.19**	**0.00**	1.83	
MC	**–9.54**	**0.28**	4.14		3.13		0.39	
MCWA	–1.10		0.41		**14.75**	**4.82**	**3.49**	**2.09**
ASP	–0.62		0.39		2.89		0.56	
NV	**–1.06**	**0.00**	**–1.01**	**0.00**	**–0.98**	**0.00**	**–1.04**	**0.00**
HUMU	7.68		**–16.48**	**0.74**	**–6.09**	**0.91**	–3.78	

[a] Habitat abbreviations are as follows: HM = herbaceous meadows, HW = herbaceous wetlands, XS = xeric shrublands, MS = mesic shrublands, ROCK = rocky areas, DD = dead and down, K = krummholz, LIMP = limber pine, LP = lodgepole pine, PP = Ponderosa pine, MDF = montane Douglas fir, RMC = riparian mixed conifer, MC = mixed conifer, MCWA = mixed conifer with aspen, ASP = aspen, NV = non-vegetated surfaces, HUMU = human-use areas.

relationship among bears across habitat factors and use ($H_6 = 8.8$, $P = 0.183$; Table 18), indicating little consistent selection of habitat factors across bears, and thus, I did not construct a combined model. For the contemporary period, distance to trails and elevation were the primary factors influencing bear use ($H_6 = 11.5$, $P = 0.075$; Table 19) with black bears typically found at lower elevations and closer to trails (Fig. 1). The classification percentage for this model was 72.6%, with the greatest likelihood of occurrence predicted around heavy human-use sites (Fig. 2). Vegetation type was an important variable in only 1 of 8 contemporary black bear models and 2 of 11 historical models, indicating a weak association with specific vegetation types for black bears in RMNP (Tables 18–19). Lastly, comparisons between black bear locations obtained from 1984–1991 (51% in human-use areas) and 2003–2006 (70% in human use areas) indicated a greater proportion of locations in human-use areas during the contemporary period (Fisher's exact $P < 0.001$).

Site-specific

I sampled 35 foraging and 8 resting locations of black bears, as well as 105 random locations throughout RMNP, during 2005 and 2006. Foraging sites were associated with classes of ground cover and aspect (Table 20), with aspect ($\chi^2 = 12.8$, $P = 0.005$; north: odds ratio = 2.8 [95% CI = 0.9–8.9]; east: odds ratio = 2.3 [95% CI = 0.7–8.0]; south: odds ratio = 0.5 [95% CI = 0.1–1.9]), grass (odds ratio = 0.966 [95% CI = 0.937–0.996]) and woody cover ($\chi^2 = 6.0$, $P = 0.014$; odds ratio = 0.917 [95% CI = 0.843–0.996]) exhibiting the strongest associations, although odds ratios for any particular aspect included 1 indicating a weak relationship. Presence of ant sites ($\chi^2 = 4.1$, $P = 0.044$; odds ratio = 1.3 [95% CI = 1.0–1.6]), logs ($\chi^2 = 4.4$, $P = 0.036$; odds ratio = 1.08 [95% CI = 1.01–1.16]), and non-vegetated areas ($\chi^2 = 3.8$, $P = 0.052$; odds ratio = 1.01 [95% CI = 1.00–1.03]) were also positively related to black bear foraging sites

Table 7.18. Percent contribution of selected variables related to black bear occurrence within individual home-ranges from 1984–1991 in Rocky Mountain National Park, Colorado. Area under curve (AUC) estimates and associated standard errors are provided for the best model for each bear.

	Percent contribution[a]								
	Aspect	Can ht	Elev	Roads	Slope	Trails	Veg	AUC	SE
Bear 1	0.0	33.1	46.1	0.0	0.0	20.7	0.0	0.811	0.045
Bear 2	0.0	0.0	85.2	0.0	0.0	14.8	0.0	0.642	0.048
Bear 3	0.0	17.7	0.0	82.3	0.0	0.0	0.0	0.710	0.048
Bear 5	62.1	0.0	0.0	37.9	0.0	0.0	0.0	0.752	0.071
Bear 8	51.2	0.0	48.8	0.0	0.0	0.0	0.0	0.736	0.047
Bear 11	0.0	0.0	0.0	98.8	1.2	0.0	0.0	0.852	0.057
Bear 12	0.0	0.0	0.0	0.0	0.0	18.9	81.1	0.767	0.050
Bear 15	0.0	0.0	1.2	98.8	0.0	0.0	0.0	0.860	0.039
Bear 17	0.0	0.0	0.0	92.9	0.0	0.0	7.1	0.756	0.072
Bear 22	0.0	0.0	0.0	0.0	37.4	62.6	0.0	0.658	0.090
Bear 24	0.0	0.0	0.0	87.5	12.5	0.0	0.0	0.889	0.036
$\bar{x}$:	10.3	4.6	16.5	45.3	4.6	10.6	8.0		

[a] Variables are as follows: Aspect = flat, north, east, south, or west facing slopes, Can Ht = height of canopy, Elev = elevation, Roads = distance to nearest road, Slope = degree of slope, Trails = distance to nearest trail, and Veg = dominant covertype at site.

Table 7.19. Percent contribution of selected variables related to black bear occurrence within individual home-ranges from 2003–2006 in Rocky Mountain National Park, Colorado. Area under curve (AUC) estimates and associated standard errors are provided for the best model for each bear.

	Percent contribution[a]								
	Aspect	Can ht	Elev	Roads	Slope	Trails	Veg	AUC	SE
Bear 2	0.0	36.5	63.5	0.0	0.0	0.0	0.0	0.656	0.044
Bear 3	0.0	0.0	5.7	0.0	0.0	94.3	0.0	0.753	0.042
Bear 4	0.0	0.0	60.1	39.9	0.0	0.0	0.0	0.692	0.050
Bear 5	0.0	0.0	93.9	6.1	0.0	0.0	0.0	0.901	0.049
Bear 6	0.0	0.0	0.0	0.0	30.2	69.8	0.0	0.819	0.038
Bear 7	0.0	0.0	24.1	0.0	75.9	0.0	0.0	0.760	0.055
Bear 9	0.0	0.0	0.0	0.0	0.0	64.2	35.8	0.821	0.065
Bear 10	0.0	29.3	0.0	0.0	0.0	70.7	0.0	0.809	0.047
$\bar{x}$[b]:	0.0C	8.2C	30.9AB	5.8C	13.3BC	37.4A	4.5C		

[a] Variables are as follows: Aspect = flat, north, east, south, or west facing slopes, Can Ht = height of canopy, Elev = elevation, Roads = distance to nearest road, Slope = degree of slope, Trails = distance to nearest trail, and Veg = dominant covertype at site.

[b] Values sharing the same letter did not differ at $\alpha = 0.10$.

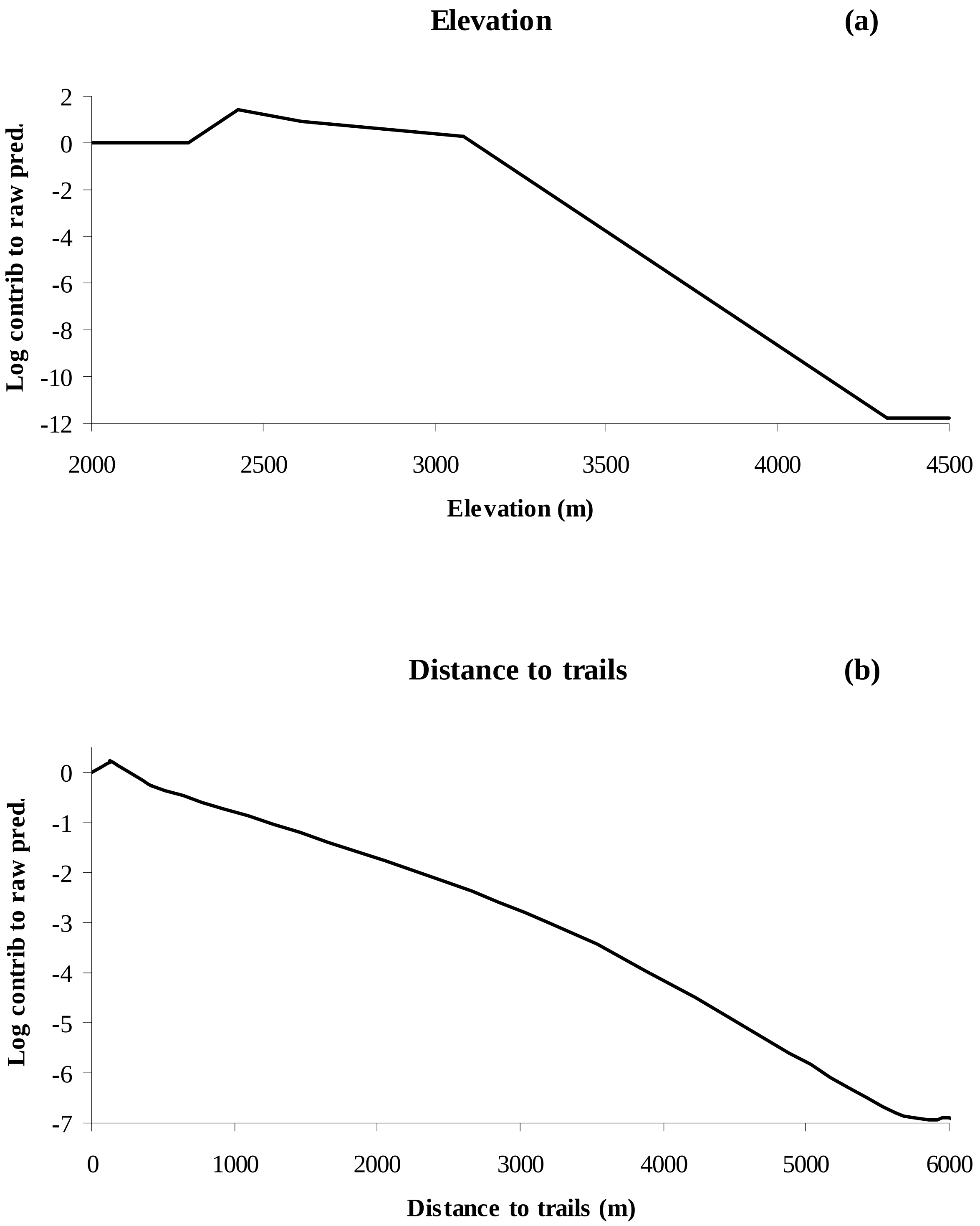

Figure 7.1. Relationships between the exponential contribution of elevation (a) and distance to trails (b) to the raw prediction score and the observed value for 9 bears from 2003–2006 in Rocky Mountain National Park, Colorado.

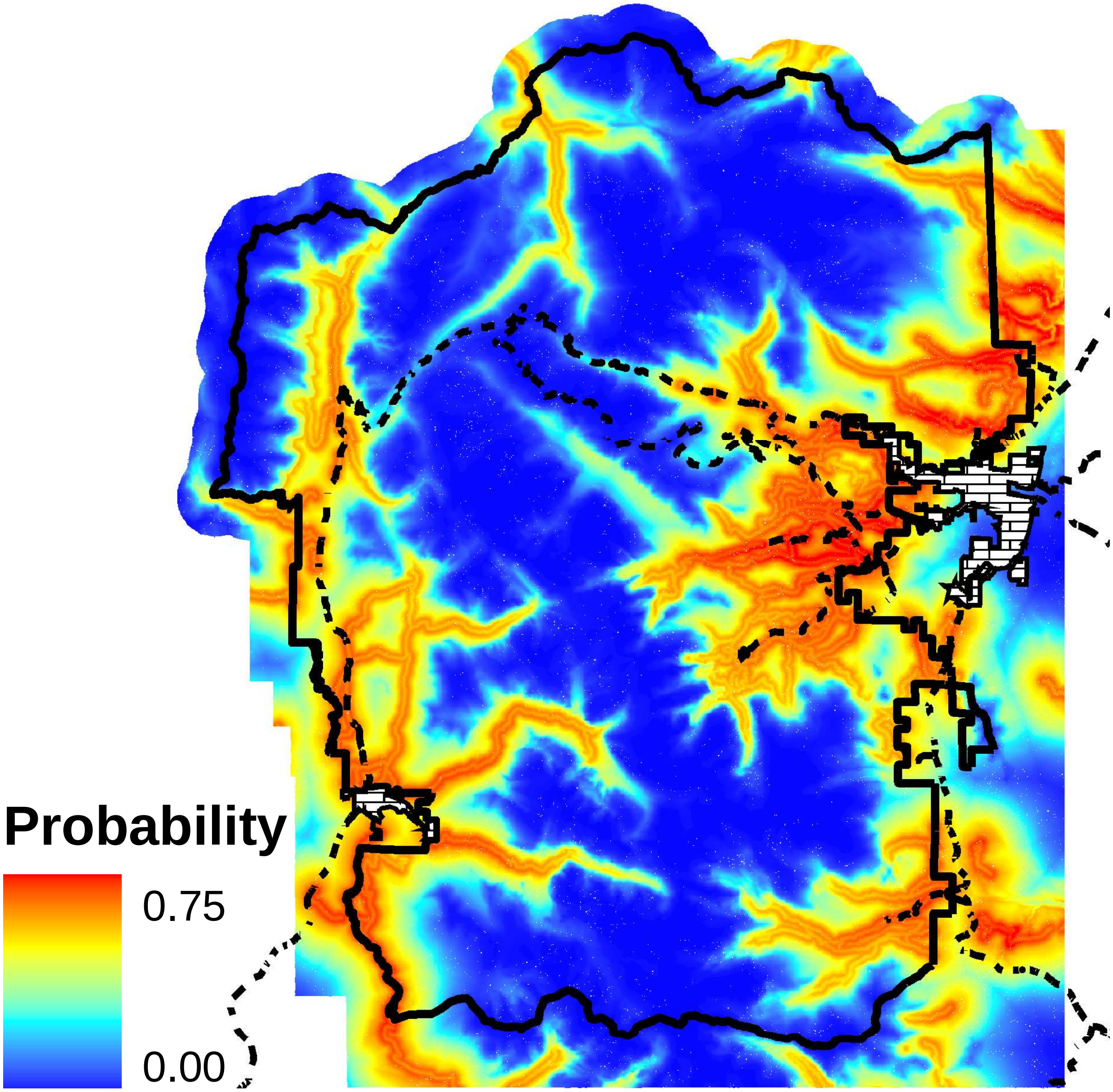

Figure 7.2. Map depicting probability of use by black bears in Rocky Mountain National Park (RMNP), Colorado from 2003–2006. Variables nested within the model include distance to trails and slope. The RMNP boundary is demarcated by a solid black line, roads are depicted by dashed lines, while white-bricked areas represent urban sites.

Table 7.20. Logistic regression results relating site-specific habitat factors at 35 foraging sites of black bears to 105 random locations throughout Rocky Mountain National Park, Colorado from 2005–2006. Values reported include likelihood ratio (for Model) and Wald (for Parameter) χ^2 statistics (χ^2) and associated *P* values (*P*), Schwartz information criterion (SIC) values, maximum rescaled generalized R^2 (R^2), percent concordance (% con), and parameter estimates (β) and associated standard errors (SE). The 3 best supported variables are in bold.

	Model					Parameter			
Variable	χ^2	*P*	SIC	R^2	% con	β	SE	χ^2	*P*
Canopy cover	2.6	0.105	164.7	0.028	57.4	0.012	0.007	2.5	0.115
Vertical cover	1.7	0.190	165.6	0.018	55.0	–0.012	0.009	1.7	0.190
Canopy height	1.0	0.318	166.3	0.011	54.4	0.048	0.048	1.0	0.323
Stem density	2.0	0.153	165.3	0.022	65.1	0.025	0.017	2.0	0.155
Basal area trees	1.3	0.251	166.0	0.014	58.2	0.010	0.009	1.3	0.251
Basal area snags	0.4	0.553	167.0	0.004	44.3	–0.009	0.015	0.3	0.562
Slope	1.5	0.228	165.9	0.015	57.9	0.026	0.022	1.5	0.228
Aspect	12.8	0.005	164.5	0.129	56.7				
North						0.766	0.316	5.9	0.015
East						0.570	0.353	2.6	0.107
South						–1.066	0.432	6.1	0.014
Ants	4.1	0.044	163.3	0.043	34.1	0.241	0.124	3.8	0.052
Logs	4.4	0.036	162.9	0.046	57.9	0.076	0.037	4.4	0.037
Grass	6.9	0.009	160.4	0.071	57.3	–0.034	0.015	6.9	0.009
Fruits	0.1	0.791	167.3	0.001	48.0	0.003	0.010	0.1	0.790
Woody	6.0	0.014	161.3	0.062	55.7	–0.087	0.042	4.2	0.040
Herbaceous	0.7	0.417	166.7	0.001	52.9	–0.013	0.016	0.6	0.426
Non-vegetated	3.8	0.052	163.6	0.039	60.7	0.014	0.007	3.7	0.054

(Table 20). The best multivariate model for foraging locations included aspect, non-vegetated ground cover, and log cover (Table 21). This model indicated greater use of sites with north ($\chi^2 = 5.3$, $P = 0.021$; β = 0.778 [SE = 0.337]; odds ratio = 3.1 [95% CI = 0.9–10.8]) and east facing aspects ($\chi^2 = 4.4$, $P = 0.036$; β = 0.789 [SE = 0.377]; odds ratio = 3.2 [95% CI = 0.9–111.9]), while southern aspects ($\chi^2 = 7.2$, $P = 0.007$; β = –1.198 [SE = 0.446]; odds ratio = 0.4 [95% CI = 0.1–1.9]) were avoided. However, odds ratios for all directions included 1 indicating a weak relationship for aspect. This model also indicated a preference for greater coverage of non-vegetated surfaces ($\chi^2 = 6.4$, $P = 0.012$; β = 0.022 [SE = 0.009]; odds ratio = 1.02 [95% CI = 1.01–1.04]) and logs ($\chi^2 = 5.6$, $P = 0.018$; β = 0.101 [SE = 0.043]; odds ratio = 1.11 [95% CI = 1.02–1.20].

Given the small number of resting sites sampled, I did construct logistic models of resting sites. Resting and foraging sites only differed (Table 3) in degree of slope ($U = 84.5$, $P = 0.083$) and percent ground cover of woody vegetation ($U = 76.0$, $P = 0.043$). Resting sites thus were similar to foraging locations in RMNP, but were associated with steeper slopes and more understory woody vegetation (Table 3).

Body condition-habitat relationships

Landscape.—For annual home-range composition, BF was negatively associated with the amount of limber pine ($F_{1,7} = 9.0$, $P = 0.020$, $R^2 = 0.564$; β = –0.937, SE = 0.312) contained in female home-ranges, while no variables were related to BCI for annual female home-ranges. During spring, aspen ($F_{1,5} = 4.7$, $P = 0.083$, $R^2 = 0.483$; β = 5.037, SE = 2.330) and Douglas fir ($F_{1,5} = 4.2$, $P = 0.095$, $R^2 = 0.459$; β = 0.564, SE = 0.274) composition were positively related to BF, while herbaceous meadows ($F_{1,5} = 4.8$, $P = 0.081$, $R^2 = 0.488$; β = –1.130, SE = 0.518) and mixed conifer ($F_{1,5} = 4.4$, $P = 0.090$, $R^2 = 0.469$; β = –0.286, SE = 0.136) stands exhibited a

Table 7.21. Summary of selected black bear habitat-use models at the site-specific scale for foraging sites in Rocky Mountain National Park, Colorado, 2005–2006. Values reported include likelihood ratio χ^2 statistics (χ^2) and associated P values (P), Schwartz information criterion (SIC) values, the difference in SIC when compared to the top models (ΔSIC), percent concordance (% con), maximum rescaled generalized R^2 (R^2), and the summation of the rank scores (Σ rank) when comparing models through ΔSIC, R^2, and % con. The preferred model is in bold.

Model[a]	χ^2	P	SIC	ΔSIC	R^2	% con	Σ rank
Aspect, non-veg, logs	**24.4**	**<0.001**	**162.75**	**0.00**	**0.236**	**76.5**	**3.0**
Aspect, non-veg, woody	22.6	<0.001	164.47	1.72	0.221	75.0	6.5
Aspect, woody, ants	22.6	<0.001	164.48	1.73	0.221	74.4	8.5

[a] Variable notation: aspect = direction of slope, non-veg = percent coverage by bare soil, duff, and leaf litter, logs = percent coverage by logs, woody = percent coverage by woody species, and ants = percent coverage by ant mounds and rocks with ants underneath.

negative association. BCI was positively related to aspen ($F_{1,5}$ = 9.2, P = 0.029, R^2 = 0.647; β = 0.607, SE = 0.200) and lodgepole pine ($F_{1,5}$ = 5.3, P = 0.070, R^2 = 0.513; β = 0.054, SE = 0.023) stands. For summer home-range composition, limber pine was negatively related to for both BF ($F_{1,7}$ = 9.2, P = 0.019, R^2 = 0.569; β = –1.065, SE = 0.350) and BCI ($F_{1,7}$ = 3.7, P = 0.098, R^2 = 0.343; β = –0.086, SE = 0.045). During autumn, human-use areas ($F_{1,7}$ = 4.9, P = 0.062, R^2 = 0.412; β = 0.236, SE = 0.107) were positively related to BF, while limber pine ($F_{1,7}$ = 7.5, P = 0.029, R^2 = 0.517; β = –0.302, SE = 0.111) exhibited a negative association; mixed conifer ($F_{1,7}$ = 3.9, P = 0.091, R^2 = 0.343; β = 0.032, SE = 0.016) composition was positively associated with BCI. No landscape metrics were associated with condition indices.

Home-range.—Use of limber pine ($F_{1,6}$ = 4.9, P = 0.069, R^2 = 0.448; β = –0.809, SE = 0.366) stands was negatively associated with BF annually, while mesic shrublands were positively associated with both BF ($F_{1,6}$ = 5.1, P = 0.065, R^2 = 0.459; β = 1.899, SE = 0.841) and BCI ($F_{1,6}$ = 8.8, P = 0.025, R^2 = 0.594; β = 0.225, SE = 0.076). During spring, mixed conifer ($F_{1,5}$ = 5.9, P = 0.060, R^2 = 0.540; β = –31.791, SE = 13.117) and limber pine ($F_{1,5}$ = 4.9, P = 0.078, R^2 = 0.494; β = –102.086, SE = 46.212) locations were negatively associated with BF; aspen ($F_{1,5}$ = 8.6, P = 0.033, R^2 = 0.631; β = 8.105, SE = 2.772) and mesic shrublands ($F_{1,5}$ = 12.8, P = 0.016, R^2 = 0.719; β = 10.070, SE = 2.818) were positively associated with BCI. No covertypes were associated with condition indices during summer. Ponderosa pine stands ($F_{1,3}$ = 7.2, P = 0.075, R^2 = 0.705; β = –31.724, SE = 11.839) were negatively associated with BF during autumn; both BF ($F_{1,3}$ = 9.2, P = 0.056, R^2 = 0.754; β = 23.100, SE = 7.620) and BCI ($F_{1,3}$ = 10.5, P = 0.048, R^2 = 0.778; β = 1.611, SE = 0.497) were positively associated with black bear use of human-use areas in autumn.

Collectively among indices, covertypes most strongly related to black bear condition annually were limber pine (negative relationship) and mesic shrublands (positive relationship). Seasonally, aspen (positive) and mixed conifer (negative) showed the strongest relationships between spring habitat use and condition, limber pine (negative) between summer use and condition, and human-use areas (positive) with black bear habitat use in autumn. Thus, among all seasons and condition indices, only aspen, mesic shrublands, and human-use areas were positively related to black bear condition in RMNP.

DISCUSSION

Black bears in RMNP were very eclectic in composition of annual and seasonal home-ranges. For contemporary and historic periods, 20 of 24 and 19 of 24 habitat types and landscape metrics were significantly over or underrepresented in home-ranges, respectively (Tables 4 and 8). Similar results were observed when only eastern or western home-ranges were considered; contemporary eastside home-ranges had 19 of 24 variables significantly over or underrepresented (Table 6), and historic eastside and westside home-ranges had 16 of 24 and 12 of 24 variables, respectively (Tables 10 and 12). Hence, there were few commonalities in the features most strongly associated with home-range composition between historical and contemporary periods. For the contemporary period, black bears tended to have more aspen, greater interspersion and juxtaposition of habitat patches, and greater Shannon’s diversity and Shannon’s evenness scores associated with home-ranges. In historic home-ranges, black bears tended to have less herbaceous meadows, krummholz, and rock habitats, more human-use and non-vegetated sites, and lower values of AWMSI. However, while there were few commonalities regarding covertypes within home-ranges, landscape metrics for both the contemporary and historical period indicated a preference for small patches and high landscape diversity (see below). Similarly, MaxEnt models included vegetation covertype in only 1 of 8 and 2 of 11 best models for contemporary and historic periods, respectively, indicating highly variable use of vegetation covertypes among black bears in RMNP. This also supports movement data of black bears in RMNP (see Chapter 1), which suggests that black bear distribution is related more to differing annual and seasonal distributions of foods rather than covertypes, *per se*. In contrast to landscape-level analyses, use of vegetation covertypes within home-ranges during the contemporary period was more consistent, as several covertypes (herbaceous meadows and wetlands, xeric shrublands, krummholz, and limber pine) were consistently avoided, likely because of negative associations with accrual of body condition and thus food sources (see below). Collectively, however, it appears that black bears in RMNP seek highly diverse ranges characterized by small patches with less regard for any particular covertype. Such selection highlights the strong seasonal and annual variation in availability of preferred foods in RMNP (see Chapter 6).

Despite this variation, patterns observed across spatial scales and relationships with black bear condition help explain associations seen within any scale of analysis. Collectively, the patterns indicated positive associations with aspen and human-use areas and negative associations with open vegetation cover types (i.e., herbaceous meadows and wetlands, xeric shrublands, rocky areas, and krummholz). Open areas were typically avoided by black bears at both landscape and home-range scales. Black bears in RMNP consumed a high proportion of insects (37.3% adjusted fecal volume; see Chapter 6), which likely contributed to their lack of association with open habitats, as ants were not found in any site-level sample plots in open habitat types (*n* = 18) in RMNP. The only open habitat used with any substantial frequency was mesic shrublands, which was positively related to accretion of both BF ($\beta = 1.9$, SE = 0.8) and BCI ($\beta = 0.2$, SE = 0.1) in black bears annually, likely due to importance in spring foods (BCI: $\beta = 10.1$, SE = 2.8). Although not significant, black bears showed a positive association with mesic shrublands for all years at the home-range scale during spring (Table 15). Typically, such areas are only used by black bears during spring and early summer when herbaceous material is most digestible and relatively high in protein (Kelleyhouse 1980, Graber and White 1983, Stubblefield 1993). All black bear locations in mesic shrublands in RMNP occurred before 24 July ($\bar{x}$ = 28 June), indicating little use of such habitats later in the year.

Similarly, aspen (0.54% of RMNP) was relatively rare in RMNP, but was consistently overrepresented in contemporary home-ranges (although not historical). Aspen was the lone covertype positively associated with black bear use annually for home-ranges (Table 14) and was also positively related to nutritional condition of black bears at both landscape (BF: $\beta = 5.0$, SE = 2.3; BCI: $\beta = 0.6$, SE = 0.2) and home-range (BCI: $\beta = 8.1$, SE = 2.8) scales. Deciduous covertypes have similarly been identified as preferred habitats in other areas (Washington, Lyons et al. 2003; Virginia, Hellgren et al. 1991; New York, Costello and Sage 1994) due to greater food abundance associated with these habitats.

Human-use areas were important for both historic and contemporary periods. Historically, this was particularly relevant when examining west-side localities, as human-use and non-vegetated surfaces were both strongly related to home-range composition (Tables 12–13), whereas east of the divide neither was overrepresented. This disparity suggests that historically, black bears may have been habituating to human-use sites west of the continental divide while maintaining their wild nature in eastern RMNP.

During the contemporary period, human-use areas were positively associated with black bear home-ranges (Tables 4 and 6), non-vegetated surfaces were included in the best occupancy model, and human-use areas were strongly related to accrual of BF (landscape scale: $\beta = 0.2$, SE = 0.1; home-range scale: $\beta = 23.1$, SE = 7.6) and BCI (home-range scale: $\beta = 1.6$, SE = 0.5) during autumn. MaxEnt models also indicated that black bears selected sites at lower elevations that were closer to trails during the contemporary period (Fig. 1); this further indicated a pattern of selection by black bears for areas that were in closer proximity to human-use sites (Fig. 2). Additionally, a greater proportion of locations were obtained in human-use areas contemporarily (contemporary = 70%, historic = 51%; Fisher's exact $P < 0.001$), and comparisons between contemporary and historic black bear diets (frequency of occurrence) indicated that anthropogenic food consumption was 15.2 times higher during the contemporary period (contemporary = 17 of 120 scats, historic = 2 of 214; Fisher's exact $P < 0.001$). Overall, these patterns highlight increased use of human-associated habitats, with black bears deriving substantial benefits (i.e., greater nutrition) from this association. Consequences of this association should include an increase in condition of black bears from the historic to the contemporary period, because resources associated with human-use areas (anthropogenic foods) are much higher in calories, carbohydrates, proteins, and fats than most natural diets (Stringham 1989). In fact, nutritional condition of black bears increased from historical levels (see Chapter 2), and in the contemporary period both greater composition of human-use sites within home-ranges (BF: $F_{1,7} = 4.9$, $P = 0.062$) and greater use of human-use sites within home-ranges (BF: $F_{1,3} = 9.2$, $P = 0.056$; BCI: $F_{1,3} = 10.5$, $P = 0.048$) during autumn (the season most closely tied to fat accretion in black bears; Pelton 2003) were positively related to black bear condition in RMNP.

Collectively, these results indicate that black bears in RMNP may be habituating to human presence, and deriving substantial resource benefits (i.e., increased condition and subsequently increase individual fitness) from this association. Although historically, black bears east of the continental divide in RMNP may have exhibited cryptic behavior and avoided heavy human-use areas (McCutchen 1990), it appears that black bears in western RMNP historically were exhibiting patterns similar to eastern black bears in the contemporary population. A further shift in black bear behavior west of the continental divide may have occurred since the historic period, as both black bears collared in western RMNP were captured within 6.4 km (diameter of mean home-range size of females from the contemporary period; see Chapter 1) of Grand Lake Village, and 4 of 7 camera sites with black bear photographs were located within this same distance (2 of the 3 other sites were within 7.8 km of Grand Lake Village). The changing distribution of black bears in RMNP towards areas with greater human influence (including selection of dens sites; Chapter 5), and increased size and productivity of black bears in RMNP (see Chapters 2 and 4), itself likely a product of increased nutrition, indicates that black bears in RMNP are altering behaviors to access high yield resources associated with human-use areas. Such changes have previously been documented in the Lake Tahoe region (Beckmann and Berger 2003 a, b), where negative bear-human encounters also increased. Recent negative bear-human encounters in RMNP, such as a black bear attack at a backcountry campsite during 2003, may further reflect increasing habituation to humans by black bears in order to exploit high yield resources (i.e., anthropogenic foods).

Black bear associations with other covertypes were far more variable and less consistent. Black bear use of mixed conifer at the landscape scale showed little consistency (Tables 4–7), and condition indices were negatively correlated with mixed conifer at both scales during spring, but positively associated during autumn. Food availability is often the overriding factor influencing black bear habitat selection (Rogers 1993) and likely influenced these differences for mixed conifer stands. The primary foods (% volume of foods ingested; Chapter 6) of black bears in RMNP were green vegetation (57.5%), insects (46.9%), and berries (31.6%) during spring, summer, and autumn, respectively. When comparing mixed conifer stands to other covertypes, mixed conifer contained substantially less green vegetation (mixed conifer = 6.9%, others = 32.2%; $U = 148.0$, $P < 0.001$) but greater cover associated with berry species (mixed conifer = 38.9%, others = 13.7%; $U = 1031.0$, $P < 0.001$) and insects (mixed conifer = 7.0%, others = 5.0%; $U = 824.5$, $P = 0.024$). Given the high volume of green vegetation in black bear diets in spring, a lack of these items might result in a negative relationship between these components and nutritional condition. Likewise, increased availability of berries and insects would likely increase use of mixed conifer stands during summer months and should lead to increased condition of black bears during autumn. Therefore, although the importance of mixed conifer appears to vary substantially depending on season, these differences appear to be related to food availability.

Limber pine nuts have been hypothesized to be an important food for black bears in RMNP (McCutchen 1996), and limber pine was positively associated with landscape models of black bear home-range attributes in RMNP (Tables 4–7). Occupancy modeling utilizing remote-sensored cameras also indicated that limber pine ($\beta = 0.306$, SE = 0.100) was an important component related to black bear occurrence in RMNP during late summer and autumn. However, nutritional condition was consistently negatively related to limber pine, and limber pine was consistently negatively related to black bear occurrence at the home-range scale in all but autumn (Tables 14–17). Limber pine nuts are consumed by black bears in RMNP during late autumn when other food sources are scarce (McCutchen 1996). Additionally, 3 of 4 limber pine sites surveyed contained ant mounds or ants under rocks (a component related to site-specific selection of black bears), while only 24 of 100 other randomly surveyed sites contained such ant sources (Fisher's exact $P = 0.053$). Ants and other insects are one of the most important food sources available to black bears in RMNP (see Chapter 6). Therefore, limber pine stands may provide foraging opportunities for insects and pine nuts during autumn when other foods may be scarce. Nonetheless, even during autumn such sites likely do not greatly benefit black bears given the negative relationship between use of limber pine stands and BF of black bears ($\beta = -0.302$, SE = 0.111).

Lodgepole pine, ponderosa pine, and Douglas fir use varied considerably depending on scale and season (Tables 4–7, 14–17). At the landscape scale, lodgepole pine was positively related to BCI during summer. Preferred use of lodgepole stands was also described previously in RMNP (Zeigenfuss 2001). Lodgepole pine stands contained a higher proportion of sites with ant sources (6 of 13) than the other habitat types combined (21 of 91 sites; Fisher's exact $P = 0.095$), and this may have influenced black bear use of such habitats. At the home-range scale, ponderosa pine was negatively correlated with BF during autumn. Negative associations with ponderosa pine sites have been documented in other areas (e.g., Mollohan et al. 1989) as such stands typically provide little cover and few food sources. Douglas fir was positively related to BF accrual of black bears at the landscape scale during spring, but reasons for increased condition associated with Douglas fir stands remains unclear. However, use of similar habitats was noted in other locations (e.g., California, Kelleyhouse 1980), and Douglas fir logs have been considered preferred sites when foraging for ants (Bull et al. 2001).

Method of analysis may also affect habitat use relationships. For example, greater amounts of krummholz were preferred in the occupancy model despite being strongly avoided by black bears (black bears were never located in krummholz). This discrepancy was likely the result of the relationship between dates sampled and elevation. In mountainous terrain, black bears frequently move higher in elevation ($\bar{x}$ elevation: krummholz = 3,461 m, SE = 1.5; limber pine = 3,125 m, SE = 8.6; other forested covertypes = 2,980, SE = 3.2) as seasons progress into summer and early autumn. These movement patterns typically mirror the ripening of soft mast (e.g., raspberry [*Rubus* spp.], chokecherry [*Prunus virginiana*]) and other food sources (Beck 1991). Because camera-trapping was conducted in late summer and early autumn, the positive association between black bears and krummholz (and limber pine) in occupancy models may merely reflect use of high elevations in this period. Consequently, whenever possible, multiple techniques should be used to assess habitat affinities, as in this project.

Although the influence of landscape metrics on black bears has not been assessed for most populations, such information has provided valuable insights into resource selection in other mammals (i.e., Virginia opossum [*Didelphis virginiana*] [Dijak and Thompson 2000]; marten [Potvin et al. 2001]). All landscape metrics positively associated with black bear home-ranges (interspersion and juxtaposition and Shannon’s evenness and diversity indices) indicated a preference for numerous patches with even distributions (Tables 4–7). Increasing patch diversity and edge in RMNP thus yielded higher quality habitats for black bears. Such a patchwork landscape provides a wide diversity of resources, which is likely more important in RMNP than in most other locations given the paucity of abundant food sources in high elevation areas (Beck 1991). Similarly, the negative association with AWMSI historically implied a preference for a more even distribution of habitat types, though it places more emphasis on the shape of the habitat patch (i.e., less edge per interior).

The use of site-specific data can also further our understanding of habitat selection at both the landscape and home-range scales. Results from foraging sites indicated a preference for northern aspects but an avoidance of southern aspects (although odds ratios indicated these were weak relationships); greater coverage by fallen logs, non-vegetated surfaces, and ant mounds and rocks with ants underneath; but less grass and woody cover (Table 20). Mesic north slopes typically have greater vegetative production (Beidleman et al. 2000). This increased understory production yields more abundant food sources and better concealment than southerly aspects. Rotten logs often harbor abundant insect and grub populations which are preferred foods (Bull et al. 2001), and are also often used as resting sites (Mollohan et al. 1989, Bull et al. 2001). Additionally, black bears preferred less woody cover at foraging sites; less woody cover likely reduces visual obstruction allowing for better visual acuity while foraging. Increased proportion of non-vegetated surfaces was also included in the best models of foraging locations (Table 21). Reasons for this are unclear but could be related to the high negative correlation between non-vegetated surfaces and grasses ($r_s = -0.616$), as grass cover was strongly avoided (Table 20) at foraging sites.

Slope and woody cover were the only variables that differed between resting and foraging locations (Table 3). These differences likely reflected the differing needs of black bears in terms of food vs. cover. For example, slope was greater for resting locations than for foraging sites. Steeper slopes likely allow black bears greater security due to inaccessibility of sites (Mollohan et al. 1989) and less visual obstruction which is more important at resting sites (Mollohan et al. 1989). Likewise, the higher woody vegetation cover I saw at resting sites also provides additional security cover (Cunningham et al. 2003). Overall, however, there were few structural or other habitat attribute differences between foraging sites and resting sites in RMNP. A similar observation was noted in mixed conifer stands in California (Kelleyhouse 1980), which suggests that black bears may simply choose the most secure location in foraging areas to rest given that they are less mobile and their energy costs for movement are greater (Robbins 1993) than species such as elk and deer, which typically have very distinct foraging and resting sites.

MANAGEMENT IMPLICATIONS

Body condition of black bears was most strongly positively influenced by aspen (spring), mesic shrublands (annually), and human-use covertypes (autumn), and negatively associated with limber pine (annually and all seasons) and mixed conifer (spring) covertypes in RMNP. This was reflected to some degree in placement of black bear home-ranges (aspen included in amounts greater than available) and to a lesser degree, use of habitat types within home-ranges (aspen used annually much more than available within home-ranges; increased use of human-use areas relative to historic black bear locations). Additionally, all habitats consistently avoided by black bears, including herbaceous meadows and wetlands, krummholz, xeric shrublands, and limber pine, were either not related or negatively associated to accrual of body condition in black bears. As indicated in analyses of foraging sites, black bears apparently specifically seek out areas with greater supplies of food regardless of habitat type; this was reflected in analyses of black bear distribution patterns as well (see Chapter 1). This also explains the consistent pattern of landscape metrics that indicate high habitat diversity and significant edge in home-range placement of black bears in RMNP. By maximizing diversity in home-ranges, black bears can likely increase the probability that important foods, which vary significantly in annual, seasonal, and spatial availability in RMNP (see Chapters 1 [movements and distribution] and 6 [foods]), are available within home-ranges. Thus management actions aimed at addressing landscape distribution and specific structures of covertypes may be more important in providing for the critical nutritional needs of black bears in RMNP than providing for any specific habitat type, *per se*, with the possible exception of aspen.

Potential management actions can produce both results, however (i.e., providing critical structure associated with foods, such as downed logs, and focusing on specific vegetation types that are positively associated with black bear condition, such as aspen). Active forest management (i.e., prescribed burning, thinning, and clearcutting of small patches), such as associated with fuels reduction programs in urban-interface areas, in a patchwork design would increase the abundance and distribution of these early successional habitats (Irwin and Hammond 1985) and facilitate the fractal structure of habitats preferred by black bears in RMNP. These management practices would be most effective on north or east facing slopes. Similarly, wildfires often burn asymmetrically, thus providing higher diversity and more edge of habitat types, as well as increased early successional habitats (with greater plant productivity) and more downed and coarse woody materials (insect habitats). Aspen stands particularly require continued disturbance to maintain their presence in the landscape (i.e., to halt succession to mixed conifer stands, which have far less value to black bears in RMNP).

The positive association between black bear condition and use of human-associated areas of RMNP is problematic for the long term viability of the black bear population in RMNP, however. Increased use of human-associated landscapes by black bears in RMNP can only ultimately negatively affect the black bear population, as bears usually lose in human-bear conflicts. Because this use is almost certainly resource (food) driven, management actions or natural disturbances that enhance the forage attributes of RMNP habitats could shift black bears away from human-use areas, maintaining the wild nature of RMNP's black bear population, while reducing human-bear conflict. As a minimum, continued prescribed burning in RMNP and a "let burn" management philosophy towards wildfire (to the extent that safety allows) can only help provide the habitat diversity and resources preferred by black bears in RMNP.

LITERATURE CITED

Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74:1313–1325.

Agresti, A. 1996. An introduction to categorical data analysis. John Wiley and Sons, New York, New York, USA.

Anderson, S. H., and K. J. Gutzwiller. 1996. Habitat evaluation methods. Pages 592–606 *in* T. A. Bookhout, editor. Research and management techniques for wildlife and habitats. Fifth edition. The Wildlife Society, Bethesda, Maryland, USA.

Apps, C. D., B. N. McLellan, T. A. Kinley, and J. P. Flaa. 2001. Scale-dependent habitat selection by mountain caribou, Columbia Mountains, British Columbia. Journal of Wildlife Management 65:65–77.

Atkinson, S. N., and M. A. Ramsay. 1995. Effects of prolonged fasting on the body composition and reproductive success of adult female polar bears (*Ursus maritimus*). Functional Ecology 9:559–567.

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

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

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

Bender, L. C., and J. G. Cook. 2005. Nutritional condition of elk in Rocky Mountain National Park. Western North American Naturalist 65:329–334.

Bender, L. C., J. G. Cook, R. C. Cook, and P. B. Hall. 2007a. Relations between nutritional condition and survival of elk in the Pacific Northwest. Wildlife Biology 13: *In press.*

Bender, L. C., L. A. Lomas, and J. Browning. 2007b. Condition, survival, and cause-specific mortality of mule deer in northcentral New Mexico. Journal of Wildlife Management 71:1118–1124.

Bender, L. C., L. A. Lomas, and T. Kamienski. 2007c. Habitat effects on condition of doe mule deer in northcentral New Mexico. Rangeland Ecology and Management 60:277–284.

Bull, E. L., T. W. Heater, and T. L. Wertz. 2001. Black bear habitat use in northeastern Oregon. Western Black Bear Workshop 7:82–91.

Cattet, M. R. L., N. A. Caulkett, M. E. Obbard, and G. B. Stenhouse. 2002. A body-condition index for ursids. Canadian Journal of Zoology 80:1156–1161.

Clark, J. D., J. E. Dunn, and K. G. Smith. 1993. A multivariate model of female black bear habitat use for a Geographic Information System. Journal of Wildlife Management 57:519–526.

Cook, R. C., J. G. Cook, D. L. Murray, P. Zager, B. K. Johnson, and M. W. Gratson. 2001. Nutritional condition models for elk: which are the most sensitive, accurate, and precise? Journal of Wildlife Management 65:988–997.

Costello, C. M., and R. W. Sage, Jr. 1994. Predicting black bear habitat selection from food abundance under 3 forest management systems. International Conference on Bear Research and Management 9:375–387.

Cottam, G., and J. T. Curtis. 1956. The use of distance measures in phytosociological sampling. Ecology 37:451–460.

Cunningham, S. C., W. B. Ballard, L. M. Monroe, M. J. Rabe, and K. D. Bristow. 2003. Black bear habitat use in burned and unburned areas, central Arizona. Wildlife Society Bulletin 31:786–792.

Davis, R. W. 2006. A GIS-based habitat model predicting elk nutritional condition in the Pacific Northwest. Dissertation, University of Illinois, Urbana, Illinois, USA.

Dijak, W. D., and F. R. Thompson, III. 2000. Landscape and edge effects on the distribution of mammalian predators in Missouri. Journal of Wildlife Management 79:204–214.

Efron, B., and R. J. Tibshirani. 1993. An introduction to the bootstrap. Chapman and Hall. New York, New York, USA.

Elkie, P. C., R. S. Rempel, and A. P. Carr. 1999. Patch Analyst User's Manual. Technical Manual TM-002, Northwest Science and Technology, Ontario Ministry of Natural Resources, Thunder Bay, Canada.

Farley, S. D., and C. T. Robbins. 1994. Development of two methods to estimate body composition of bears. Canadian Journal of Zoology 72:220–226.

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.

Fortin, D., J. M. Fryxell, L. O'Brodovich, and D. Frandsen. 2003. Foraging ecology of bison at the landscape and plant community levels: the applicability of energy maximization principles. Oecologia 134:219–227.

Franzmann, A. W. 1985. Assessment of nutritional status. Pages 239–260 *in* R. J. Hudson and R. G. White, editors. Bioenergetics of wild herbivores. CRC Press, Boca Raton, Florida, USA.

Freedman, A. H., K. M. Portier, and M. E. Sunquist. 2003. Life history analysis for black bears (*Ursus americanus*) in a changing demographic landscape. Ecological Modelling 167:47–64.

Gaillard, J.-M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toïgo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31:367–393.

Gau, R. J., and R. Case. 1999. Evaluating nutritional condition of grizzly bears via select blood parameters. Journal of Wildlife Management 63:286–291.

Gau, R. J., and R. Case. 2002. Evaluating nutritional condition of grizzly bears via ^{15}N signatures and insulin-like growth factor-1. Ursus 13:285–291.

Graber, D. M., and M. White. 1983. Black bear food habits in Yosemite National Park. International Conference on Bear Research and Management 5:1–10.

Hanks, J. 1981. Characterization of population condition. Pages 47–73 *in* C. W. Fowler and T. D. Smith, editors. Dynamics of large mammal populations. The Blackburn Press, Caldwell, New Jersey, USA.

Hansen, J. A., S. L. Garman, B. Marks, and D. L. Urban. 1993. An approach for managing vertebrate diversity across multiple-use landscapes. Ecological Applications 3:481–496.

Hellgren, E. C., M. R. Vaughan, and D. F. Stauffer. 1991. Macrohabitat use by black bears in a southeastern wetland. Journal of Wildlife Management 55:442–448.

Herrero, S. 1983. Social behaviour of black bears at a garbage dump in Jasper National Park. International Conference on Bear Research and Management 5:54–70.

Hilderbrand, G. V., S. D. Farley, and C. T. Robbins. 1998. Predicting body condition of bears via two field methods. Journal of Wildlife Management 62:406–409.

Hosmer, D. W., and S. Lemeshow. 2000. Applied logistic regression. John Wiley and Sons, New York, New York, USA.

Irwin, L. L., and F. M. Hammond. 1985. Managing black bear habitats for food items in Wyoming. Wildlife Society Bulletin 13:477–483.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Jones, P. F., and R. J. Hudson. 2002. Winter habitat selection at three spatial scales by American elk, *Cervus elaphus*, in west-central Alberta. The Canadian Field-Naturalist 116:183–191.

Keating, K. A., and S. Cherry. 2004. Use and interpretation of logistic regression in habitat-selection studies. Journal of Wildlife Management 68:774–789.

Kelleyhouse, D. G. 1980. Habitat utilization by black bears in northern California. International Conference on Bear Research and Management 3:221–228.

Kotliar, N. B., and J. A. Wiens. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. Oikos 59:253–260.

Levy, E. E., and E. A. Madden. 1933. The point method of pasture analysis. New Zealand Journal of Agricultural Research 46:267–279.

Link, W. A., and R. J. Barker. 2006. Model weights and the foundations of multimodel inference. Ecology 87:2626–2635.

Linke, J., S. E. Franklin, F. Huettmann, and G. B. Stenhouse. 2005. Seismic cutlines, changing landscape metrics and grizzly bear landscape use in Alberta. Landscape Ecology 20:811–826.

Lofroth, E. C. 1993. Scale dependent analysis of habitat selection by marten in the sub-boreal spruce biogeoclimatic zone. Thesis, Simon Fraser University, Burnaby, British Columbia, Canada.

Lomas, L. A., and L. C. Bender. 2007. Survival and cause-specific mortality of neonatal mule deer fawns, north-central New Mexico. Journal of Wildlife Management 71:884–894.

Lord, J. M., and D. H. Norton. 1990. Spatial scale and the concept of fragmentation. Conservation Biology 4:197–202.

Lyons, A. L., W. L. Gaines, and C. Servheen. 2003. Black bear resource selection in the northeast Cascades, Washington. Biological Conservation 113:55–62.

MacKenzie, D. I., J. D. Nichols, J. E. Hines, M. G. Knutson, and A. B. Franklin. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. Ecology 84:2200–2207.

MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2005. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Academic Press, San Diego, California, USA.

McCarthy, T. M., and R. J. Seavoy. 1994. Reducing nonsport losses attributable to food conditioning: human and bear behavior modification in an urban environment. International Conference on Bear Research and Management 9:75–84.

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.

McCutchen, H. E. 1996. Limber pine and bears. Great Basin Naturalist 56:90–92.

McLoughlin, P. D., S. H. Ferguson, and F. Messier. 2000. Intraspecific variation in home range overlap with habitat quality: a comparison among brown bear populations. Evolutionary Ecology 14:39–60.

Mollohan, C., W. W. Brady, and A. L. LeCount. 1989. Habitat use of an Arizona ponderosa pine-mixed conifer forest by female black bears. Western Journal of Applied Forestry 4:6–10.

Mysterud, A., P. K. Larsen, R. A. Ims, and E. Østbye. 1999. Habitat selection by roe deer and sheep: does habitat ranking reflect resource availability? Canadian Journal of Zoology 77:776–783.

Nagelkerke, N. J. D. 1991. A note on a general definition of the coefficient of determination. Biometrika 78:691–692.

National Park Service. 1988. Management policies. U. S. Department of the Interior, Washington D. C., USA.

Noyce, K. V., P. L. Coy, and D. L. Garshelis. 2002. Bone prominence and skin-fold thickness as predictors of body fat and reproduction in American black bears. Ursus 13:275–284.

O'Neill, R. V., B. T. Milne, M. G. Turner, and R. H. Gardner. 1988. Resource utilization scales and landscape pattern. Landscape Ecology 2:63–69.

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

Pedlar, J. H., L. Fahrig, and H. G. Merriam. 1997. Raccoon habitat use at 2 spatial scales. Journal of Wildlife Management 61:102–112.

Peirce, K. N., and L. J. Van Daele. 2006. Use of a garbage dump by brown bears in Dillingham, Alaska. Ursus 17:165–177.

Pelton, M. R. 2003. Black bear (*Ursus americanus*). Pages 547–555 *in* G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, editors. Wild mammals of North America: biology, management, and conservation. Second edition, revised. The Johns Hopkins University Press, Baltimore, Maryland, USA.

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

Potvin, F., K. Lowell, M-J Fortin, and L. Bélanger. 2001. How to test habitat selection at the home range scale: a resampling random windows technique. Ecoscience 8:399–406.

Ritchie, M. E. 1998. Scale-dependent foraging and patch choice in fractal environments. Evolutionary Ecology 12:309–330.

Robbins, C. T. 1993. Wildlife feeding and nutrition. Second edition. Academic Press, San Diego, California, USA.

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.

Rogers, L. L. 1993. The role of habitat quality in the natural regulation of black bear populations. Proceedings of the Western Black Bear Conference 4:95–102.

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.

Samson, C., and J. Huot. 1998. Movements of female black bears in relation to landscape vegetation type in southern Québec. Journal of Wildlife Management 62:718–727.

Stringham, S. F. 1989. Demographic consequences of bears eating garbage at dumps: an overview. Pages 35–42 *in* M. Bromley, editor. Bear–people conflicts—Proceedings of a symposium on management strategies. Northwest Territories Department of Renewable Resources, Yellowknife, Northwest Territories, Canada.

Stubblefield, C. H. 1993. Food habits of black bear in the San Gabriel Mountains of southern California. The Southwestern Naturalist 38:290–293.

Weir, R. D., and A. S. Harestad. 2003. Scale-dependent habitat selectivity by fishers in south-central British Columbia. Journal of Wildlife Management 67:73–82.

Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology 3:385–397.

With, K. A. 1994. Using fractal analysis to assess how species perceive landscape structure. Landscape Ecology 9:25–36.

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

Zeigenfuss, L. C. 2001. Ecology of black bears in Rocky Mountain National Park: an analysis of population dynamics, diet, and habitat selection (1985–1991). Unpublished report, U.S. National Park Service, Rocky Mountain National Park, Colorado, USA.

Acknowledgments. We thank Rocky Mountain National Park, the U.S. Geological Survey, New Mexico State University, and the New Mexico Agricultural Experiment Station for funding this project. We thank Dr. Terry Terrell of RMNP, whose efforts made this project possible, and L. Zeigenfuss for providing historical data for RMNP's bear population. We further thank all the staff at RMNP, especially Judy Visty and Cheri Yost, and all the RMNP volunteers who have aided in data collection and other support of this project. In particular, we thank Lyle and Marlys Polson, Eric Dreyer, Clark Letter, Amanda Gwaltney, Kaiyote Snow, and Hank and Linda Fineberg for countless hours of volunteer assistance. Sean Eckert, Stephanie Graham, Heather Halbritter, Brock Hoenes, Barb Keller, and Mat Levine provided excellent field assistance. Further, we thank McGregor Ranch for providing convenient access through their property. We also thank Terrell "Red" Baker, Jon Boren, Andres Cibils, and Raul Valdez for reviewing all seven chapters of this report. This project provided the basis for R. Baldwin's Dissertation for the Degree of Doctor of Philosophy in Wildlife Biology in the Department of Animal and Range Sciences at New Mexico State University.

APPENDIX.—LITERATURE REVIEW

General information

The distribution of black bears (*Ursus americanus*) is more widespread than other ursids in North America, covering much of the U.S., Canada, and parts of northern Mexico (Pelton 2003). Nonetheless, their current range has been reduced by approximately 38% (Pelton and van Manen 1994) and is only 10% of their historical range in southeastern U.S. (Pelton 2003, Maehr 1984, Garshelis 1990, Jones et al. 1998). The current black bear population estimate ranges from 514,081–547,951 but does not include estimates from Alaska, Idaho, South Dakota, Texas, Wyoming, New Brunswick, Northwest Territories, Nova Scotia, Saskatchewan, or Mexico, so this number would be somewhat higher (Pelton et al. 1999).

Coloration and size can vary for black bears depending on their geographical location. The typical coloration is black with a brown muzzle in the eastern U.S. and brown in the western U.S. (Rounds 1987). However, many variations exist including all black, blond (northern California, eastern Washington, Idaho, Montana, Alberta, and Saskatchewan), white (Kermodes bear; coast of central British Columbia), blue-gray (glacier bear; Jonkel 1978), and occasionally, some bears are seen with a white blaze on their chest (Rounds 1987). The difference in coloration appears to be a cryptic response with bears in dense forest habitats exhibiting the black phase, while those in more open forests and associated habitats exhibit a lighter phase (Rounds 1987).

The average weight of adult female black bears typically ranges from 40–200 kg and from 100–300 kg for adult males (Pelton 2000). Bears in Rocky Mountain National Park (RMNP), Colorado, historically fell in the lower end of the average weight range (55 kg/adult female: 80 kg/adult male; Zeigenfuss 2001). Although heaviest individuals are typically found in Pennsylvania and New York, skull measurements indicate that in the eastern U.S., larger bears are found in southern localities (i.e., Louisiana and Mississippi), while smaller bears are found further north (i.e., Quebec; Kennedy et al. 2002). This size difference was most influenced by mean January and July temperatures, precipitation, and actual evapotranspiration; these are all factors either directly or indirectly associated with vegetative productivity. Elevations in RMNP range from 2,657–4,343 m (Zeigenfuss 2001). As with more northern latitudes, higher elevations are typically associated with lower vegetative productivity and provide a likely explanation for the small body sizes observed in RMNP.

Reproduction

Black bears are polygynous with the breeding season typically occurring in June and July, but can start as early as late May and extend to mid-August (Jonkel and Cowan 1971). Black bears exhibit delayed implantation; blastocysts do not implant until late November or early December (Wimsatt 1963). In some situations, the physical condition of the pregnant female may not be good enough to support offspring. In these situations, the blastocysts will not implant and will be reabsorbed by the bear (Elowe and Dodge 1989, Hellgren et al. 1990).

Average age of first reproduction for females typically occurs between 3–4 years but can range from 2–7 years, while males generally become reproductively active at 3–4 years of age (Pelton 2000). In RMNP, average age of first reproduction for females was approximately 7 years (Zeigenfuss 2001). Similar investigations in relatively close locales found that the average age of first reproduction was 4.7 years in western Colorado (Beck 1991) and 5.5 years in New Mexico (Costello et al. 2001). Age of first reproduction for females appears to be directly influenced by body size (Beecham 1980, Rogers 1976, 1987, Kolenosky 1990, Beck 1991, Samson and Huot 1995) and indirectly by nutrition (Rogers 1976), as nutrition plays a primary role in determining body size. Beecham (1980) and Rogers (1977, 1987) proposed that body size was a primary factor in determining age of first reproduction. Beck (1991) found the same general results although minimum weights appeared to differ across broad geographic localities. Because of this, he suggested that certain factors such as genetic differences in growth rate, social dominance, and variation in available microhabitats may all influence age of first reproduction, while Rausch (1961) suggested that latitude plays an important role, as greater latitudes typically result in shorter growing seasons and less food biomass. Nonetheless, body size of bears in RMNP is small and is likely a primary factor in the greater age of primiparity observed historically.

Late onset of reproductive activity is also affected by nutrition, as years of berry and hard mast failure have resulted in delayed estrus for primiparous females (Jonkel and Cowan 1971, Rogers 1976, Eiler et al. 1989, Elowe and Dodge 1989, Noyce and Garshelis 1994). In a related study, Costello et al. (2001) noted that age of first reproduction was greater following years of poor mast production, although this figure was not significant, likely due to small sample sizes. Hard mast crops are essentially nonexistent in RMNP and other food sources (such as berries) may not be abundant enough to allow the local population to attain minimum weight thresholds needed to produce cubs at typical ages (3–4; Pelton 2000) or at typical litter sizes (1.8–2.4; Beck 1991). Therefore, the effect of inadequate nutrition on body size suggests that a lack of abundant food resources may limit population growth in RMNP.

Cubs are born in dens in late January and early February and are small (0.2–0.3 kg), blind, and hairless when born (Pelton 2000). Sex ratios are typically 1:1 at birth with litter sizes that generally range from 1–3 (Pelton 2000). However, litters up to 5 are possible (Jonkel and

Cowan 1971, Alt 1981). The number of cubs in a litter can vary, but are typically less in western states (2.4, 2.5, 2.2, and 1.8 cubs/litter in eastern states, Great Lakes region, Alaska, and western states, respectively; Beck 1991). Average litter size for RMNP was 1.7 (McCutchen 1993). Several factors related to body condition (including body weight, habitat quality, and overall nutrition) have been implicated in influencing litter sizes (Jonkel and Cowan 1971, Beecham 1980, Rogers 1987, Alt 1989, Elowe and Dodge 1989, Stringham 1990, Schwartz and Franzmann 1991). This is particularly pronounced when dealing with areas that contain supplemental food sources such as garbage dumps and urban-interface areas (Rogers 1987, Alt 1989, Beckmann and Berger 2003b). In fact, in a study conducted on grizzly bears (*Ursus arctos*) in Yellowstone National Park, Stringham (1986) found that average litter sizes decreased by 17% once the dump was closed. These artificial food sources may be key when determining increased cub production as natural food production appears to influence litter size only in extreme situations (Rogers 1987, Beck 1991, McLaughlin et al. 1994, Noyce and Garshelis 1994). If black bears are able to supplement their typical diet with alternative foods (including human-related sources such as dumps and corn fields), then a decrease in typical foods will likely have little effect on litter size (Kasbohm et al. 1996, McDonald and Fuller 2001). Nonetheless, food limitations may be reality for bears in RMNP and alternative food sources are not readily available (lack of garbage dump, crop fields, dumpsters on park are mostly bear proof). Therefore, a lack of abundant foods is likely limiting litter sizes for bears at RMNP.

The interval between successive breeding occasions for females is typically 2 years (Pelton 2003). However, if a year of poor food production occurs, bears may forego reproduction for that year (Jonkel and Cowan 1971, Rogers 1976, LeCount 1982, Young and Ruff 1982, Eiler et al. 1989, Elowe and Dodge 1989, Hellgren et al. 1990, Beck 1991, Schwartz and Franzmann 1991, Costello et al. 2003), thereby leading to a synchronization of reproduction in subsequent years (Free and McCaffrey 1972, Lindzey et al. 1976, Lindzey and Meslow 1977a, McLaughlin et al. 1994). In some extreme cases, litters in successive years are possible, though they likely occur due to a loss of the entire litter early in the summer or to estrangement of cubs just before denning (LeCount 1983b, Alt 1989). The time for successive breeding intervals for bears in RMNP has not been reported but is believed to be 2–3 years.

Survival

Cub survival rates vary dramatically across geographic locations with values ranging from 0.45 in northern Alaska (Bertram and Vivion 2002) to 0.94 in northern Wisconsin (Massopust 1984). These rates appear to depend on a number of factors including habitat quality (Beecham 1980, Rogers 1987), spring nutrition (Schwartz and Franzmann 1991, Costello et al. 2003), unspecified social regulation (LeCount 1982), experience of the mother (Elowe and Dodge 1989, Beck 1991), spring weather (Alt 1984, Beck 1991, Oli et al. 1997), predator numbers (including conspecifics; LeCount 1987, Rogers 1987, Beck 1991) and fall mast abundance (Eiler et al. 1989, Elowe and Dodge 1989, Beck 1991, Costello et al. 2003) that directly relate to size and body condition of females (Noyce and Garshelis 1994). Cub survival in RMNP fell below these levels (0.40 ± 0.16; Zeigenfuss 2001). McCutchen (1993) implicated starvation and cannibalism as the primary mortality factors for cubs at RMNP, but other factors such as habitat quality, body condition, and researcher disturbance (see Linnell et al. 2000 for review) could be responsible as well.

Cub survival has been implicated as a primary factor regulating bear populations (Fuller 1993, Powell et al. 1996) and is therefore a factor important to bear managers (Beck 1991, McDonald and Fuller 1998). However, other researchers have found adult survival (particularly female) to be the primary factor influencing population dynamics of black (Freedman et al. 2003), grizzly (Eberhardt 1990, Wielgus et al. 2001), and polar bears (*Ursus maritimus*; Taylor et al. 1987, Eberhardt 1990) due to its influence on cubs and cub survival (Bunnell and Tait 1980, 1985, McLellan and Shackleton 1988, Mykytka and Pelton 1990, Hellgren and Maehr 1993). Recent work on large herbivores may provide some insight into this debate. Gaillard et al. (1998, 2000) reported high elasticity values for adult large herbivores, while low values were observed for juveniles, suggesting that adult survival is more important in influencing population growth. However, temporal variation (determined by coefficient of variation) is much greater for juveniles, thereby superceding the influence of elasticity. Black bears exhibit similar variability in annual cub production (Beck 1991), and therefore, likely influence population growth in a similar manner. Nonetheless, adult female survival is an important factor in regulating population growth, particularly in hunted populations where hunter kills can significantly increase mortality (e.g., Powell at al. 1996, Beringer et al. 1998) thus placing a greater influence on adult survival (Gaillard et al. 2000).

As suggested, adult survival rates seem to vary primarily due to human-related mortality. In non-exploited populations, survival of adult females is high (e.g., 0.96, Beck 1991; 0.94, Doan-Crider and Hellgren 1996), while it is somewhat lower for hunted populations (e.g., 0.85 and 0.89; Schwartz and Franzmann 1991). Males follow this same trend but typically have lower survival rates (mean survival = 86% for females, 73% for males; Kasbohm 1994; but see Powell et al. 1996) due to the fact that they have larger home-ranges, travel greater distances, and are more aggressive (Beecham 1980, Beringer et al. 1998). Average yearly survivorship for adults on RMNP was 0.84 ± 0.07 from 1984–1991 (Zeigenfuss 2001). This falls within the range typically expected for adult bears and suggests that cub mortality and reproductive limitations are more likely factors limiting population growth at RMNP.

Survival rates of subadults show much variation, but follow the same pattern as adults in that males typically have higher mortality than females. Reported survival rates for females typically range from 0.81 (Kolenosky 1986) to 0.94 (Beck 1991; but see Beringer et al. 1998) while those for subadult males can be as low as 0.265 (Beringer et al. 1998). Reasons for increased subadult male mortality are similar to those reported earlier but include added components such as dispersal, incautious behavior, and intraspecific harassment and killing (Beck 1991, Schwartz and Franzmann 1991, 1992). Yearling survival is generally lower than adult and subadult survival with reported rates ranging from 0.25 for yearling males (Elowe and Dodge 1989) to 0.94 for all yearlings combined (Beck 1991). No survival estimates for subadults and yearlings have been reported for RMNP.

There are numerous causes of mortality for black bears but most are human-caused, particularly in hunted populations (Bunnell and Tait 1985, Schwartz and Franzmann 1991, 1992, Beringer et al. 1998, Pelton 2003). Both legal and illegal hunting can serve as significant sources of mortality. Powell et al. (1996) found that 20% of mortality at Pisgah Bear Sanctuary, North Carolina was from legal hunting while 13% was from poaching, and Beck (1991) found a large illegal harvest of subadult males in west-central Colorado. Other sources of human-induced mortality include depredation control and vehicle and train collisions (Wooding and Brady 1987, Brandenburg 1996, Miller and Tutterrow 1999, Costello et al. 2001, Van Why and Chamberlain 2002, Pelton 2003, Rogers 1987). Natural mortality primarily is observed from intra- and inter-specific predation (Kemp 1976, LeCount 1987, Mattson et al. 1992, Costello et al. 2001, Gunther et al. 2002), starvation (Costello et al. 2001, Pelton 2000), and old age (Pelton

2003), but is less of a factor in hunted populations. Pelton (2003) reported several neoplastic, rickettsial, viral, and bacterial diseases that infect black bears, but noted that none played a major role in population regulation.

Population estimation

Appropriate estimates of population size for black bears are important in assessing trends in populations, understanding dynamics of a population, and in establishing hunting quotas (Miller et al. 1997). However, these estimates are difficult to attain for bears due to their low population densities, secretive nature, and use of relatively inaccessible habitat (McCutchen 1990, Costello et al. 2001, Pelton 2003). Many techniques have been used to determine bear densities, but traditional mark/recapture techniques have been used most frequently (e.g., Lindzey and Meslow 1977a, Young and Ruff 1982, Miller et al. 1987, Clark and Smith 1994). However, results from mark/recapture are often biased because they do not meet one or more of the assumptions or do not clearly delineate the area the population is using (Miller et al. 1997, Pelton 2003). In recent years, more “modern” techniques have been developed to better meet these assumptions. Some of the more promising techniques include mark-resight through use of cameras (Beck 1997, Grogan and Lindzey 1999, Martorello et al. 2001, Moruzzi et al. 2002), dogs (Akenson 2001), telemetry (Miller et al. 1997), ingested biomarkers (Garshelis and Visser 1997), and DNA mark-recapture through fecal samples and hair snaring (Woods et al. 1999, Murphy et al. 2000, Hirth et al. 2002, Boersen et al. 2003). These techniques may be more realistic and/or less biased than traditional capture methods but still have downfalls. For mark-resight, camera traps can be expensive, require large sample sizes, and still maintain a potential negative bias through the use of bait (Noyce et al. 2001, Moruzzi et al. 2002); use of dogs requires easily accessible localities and drier climates, while mark-resight combined with telemetry can be cost prohibitive (Akenson 2001). Estimates derived from ingested biomarkers are most accurate with several years of data collection and are most appropriate for hunted populations (Garshelis and Visser 1997), while DNA profiling often results in missed "captures" due to insufficient availability of genetic material from samples. It can also be quite expensive, particularly when used in areas with both black and brown bears (Woods et al. 1999).

Harvest data are extensively used by state wildlife agencies to assess population sizes in many states, although these data are not usually reliable as sex and age composition of harvested animals are usually biased by a number of factors (changes in weather and food availability [Lindzey et al. 1983]; different growth rates across populations [Caughley 1974, Harris and Metzgar 1987]; difference in methods, season, selectivity, and number of hunters [Kolenosky 1986, Litvaitis and Kane 1994, Kohlmann et al. 1999]). In fact, strong evidence suggests that mortality does not accurately represent population trends (Pelton and van Manen 1996, Garshelis and Visser 1997, Garshelis 2002). Due to limitations of each of the different techniques for estimating population size, it is recommended that several different strategies be employed to more accurately assess population size (Pelton 2003).

Density estimates vary widely across their geographical distributions. This variation is likely due to differences in methodology, as well as differences in quality of habitat and bear populations (Beck 1991, Miller et al. 1997, Pelton 2003). Densities of < 50 bear/100 km^2 and > 10 bear/100 km^2 are typically observed (Beck 1991) but extremes of 1.80 bears/100 km^2 (Grogan and Lindzey 1999) and 149 bears/100 km^2 have been reported (Lindzey and Meslow 1977a). Density estimates for RMNP (excluding alpine locations) are 2 bears/100 km^2 for the east side and 2.2 bears/100 km^2 for the west side (Zeigenfuss 2001). These estimates are approximately equal to the lowest reported densities for black bears (Grogan and Lindzey 1999) and suggest that habitat in RMNP is marginal for bears, although little is known about the relationship of habitat quality and density of bears (Beck 1991, Garshelis 2002). Estimates for other geographically similar populations are 12–16 bears/100 km^2 for west-central Colorado (Beck 1991), 36 bears/100 km^2 for northwestern Colorado (Beck 1995), 8.1 bears/100 km^2 and 39.0 bears/100 km^2 for 2 areas in north-central Colorado (Beck 1997), 2.54 bears/100 km^2 in southeastern Wyoming (Grogan and Lindzey 1999), and 17 bears/100 km^2 in northern New Mexico (Costello et al. 2001).

Population indices are alternatives that provide less costly and less time consuming alternatives to density estimates, but are also less accurate and effective (Anderson 2001, Pelton 2003). Much discussion has recently occurred on the validity of population trends derived from indices (see Anderson 2001, 2003, Engeman 2003). Nonetheless, population indices are likely to continue to be used as they are easier and less expensive alternatives to population estimates. Population indices used to monitor bear trends include scent stations (Lindzey et al. 1977), bait stations (Carlock 1986, Miller et al. 1995, Rice et al. 2001), track and scat observations (Pelton 1972, Kendall et al. 1992, Clevenger and Purroy 1996, Valdmann et al. 2001), and tree markings (Burst and Pelton 1983). However, only bait station indices and sign surveys appear to have promise in determining population trends in bears (Clevenger and Purroy 1996, Pelton 2003), though determination of individuals from track dimensions can yield minimum population sizes (Valdmann et al. 2001).

It is interesting to note that natural bear mortality in completely unexploited populations occurs through density-dependent regulation (Taylor 1994, Garshelis 2002), but for density-dependent mortality of adults to occur, populations must be at or near carrying capacity (Fowler

1981; though density can have a regulatory role in juvenile survival, Gaillard et al. 1998). However, few current bear populations are at this level (Rogers 1993, Taylor 1994, Garshelis 2002). Much effort is spent on the issue of density dependence and population regulation. However, Sargeant and Ruff (2001) point out that it might be more profitable to address factors that limit population growth in low density populations. Rocky Mountain National Park is a low density population and provides an interesting location to assess factors that influence bear mortality and production that limit their population growth.

Home-range

Knowledge of the spacing and distribution of bears can lead to a greater understanding of how they are using available resources. Determining home-range size and the degree of overlap of home-ranges provides a first step in understanding this relationship. Home-range shape and size is influenced by many factors including abundance and distribution of foods (Lindzey and Meslow 1977b, Garshelis and Pelton 1981, Rogers 1987, Elowe and Dodge 1989, Schoen 1990, Schwartz and Franzmann 1991, Schooley et al. 1994a, Powell et al. 1997, Samson and Huot 1998, Koehler and Pierce 2003), population densities (Alt et al. 1980, McLoughlin et al. 2000, Oli et al. 2002, Pelton 2003), sex and age class of individuals (Jonkel and Cowan 1971, Poelker and Hartwell 1973, Lindzey and Meslow 1977b, Alt et al. 1980, Rogers 1987, Powell et al. 1997, Hirsch et al. 1999, Koehler and Pierce 2003), social status (Alt et al. 1980, Bunnell and Tait 1981, Powell et al. 1997, Koehler and Pierce 2003), and the technique and methodology used to determine the bear's home-range (White and Garrott 1990, Powell 2000, Pelton 2003). Because of the dynamic interaction of these factors, there can be a large variation in the size of black bear home-ranges. Home-range sizes are almost always larger for males than females (typical range

= 5–49 km^2 for females, 22–1,721 km^2 for males; Pelton 2000), although this difference is not always as pronounced (e.g., Lindzey and Meslow 1977b, Garshelis and Pelton 1981). Subadult home-ranges are generally somewhat smaller (Alt et al. 1980). Average home-range size for female bears in RMNP was 53.9 km^2 while male bears averaged 35.6 km^2 (Zeigenfuss 2001). There was no significant difference in home-range size on the east and west sides of RMNP for females, but there was for males (13.1 km^2 on east side, 58 km^2 on west side; Zeigenfuss 2001). This difference was attributed to small sample sizes and a disproportionately large number of collared subadult males. Nonetheless, the home-ranges reported for females in RMNP were larger than those reported for other black bear populations. More than any other factor, habitat quality and therefore, abundance and distribution of food, have been linked to home-range size (Lindzey and Meslow 1977b, Reynolds and Beecham 1980). As reported earlier, the lower the quality of habitat, the greater the home-range size. Therefore, these large home-range sizes suggest that a lack of abundant food sources is a primary factor limiting productivity of bears in RMNP.

The degree of home-range overlap in black bears varies considerably depending upon sex and location. Males generally have home-ranges that overlap with other males and females (but see Jonkel and Cowan 1971, Poelker and Hartwell 1973), although territoriality may be expressed during the breeding season (Wooding and Hardisky 1994). In contrast, the degree of overlap of female home-ranges is quite variable with some studies showing extensive home-range overlap (e.g., Amstrup and Beecham 1976, Lindzey and Meslow 1977b, Reynolds and Beecham 1980, Garshelis and Pelton 1981, Beck 1991, Wooding and Hardisky 1994, Hirsch et al. 1999, Oli et al. 2002) while others show little (Jonkel and Cowan 1971, Young and Ruff 1982, Pelchat and Ruff 1986, Rogers 1987, McCutchen 1990). Several factors have been implicated in affecting the degree of home-range overlap in mammals including presence of altricial young (Wolff 1997, Wolff and Peterson 1998), genetic relatedness (Jonkel and Cowan 1971, Lindzey and Meslow 1977b, Pelchat and Ruff 1986, Rogers 1987), and habitat quality (Reynolds and Beecham 1980, Garshelis and Pelton 1981, Powell 1987, Rogers 1987, Hellgren and Vaughn 1990, McLoughlin et al. 2000, Oli et al. 2002). The first alternative implies that female bears should be territorial to reduce the threat of infanticide by other females (Wolff 1997, Wolff and Peterson 1998), although there is little evidence to suggest that this applies to bears. For example, in brown bears, a few instances have been recorded of unrelated females killing other cubs. However, most occurred in areas where bears expressed a lack of territoriality (McLoughlin et al. 2000), while for black bears, most studies have shown moderate to extensive overlap between females, suggesting that infanticide plays little role in the degree of home-range overlap.

Several authors have suggested that females with large degrees of home-range overlap are genetically related (e.g., Lindzey and Meslow 1977b, Pelchat and Ruff 1986, Rogers 1987, Oli et al. 2002). However, Schenk et al. (1998) found that females were not overtly related to other females with overlapping home-ranges; McLoughlin et al. (2000) found the same general results for brown bears. Therefore, although related females in some regions may share portions of overlapping home-ranges, available evidence does not suggest that relatedness is the overriding factor.

The third potential factor influencing home-range overlap appears to be the most likely explanation. Territoriality models have been proposed by Carpenter and MacMillen (1976) and Maher and Lott (2000) that suggest that territoriality is reduced when food resources are either abundant or very limited. However, territoriality is present when these resources fall at an intermediate level. Although there is no direct quantitative comparison between food abundance and home-range overlap across studies of black bears, McLoughlin et al. (2000) were able to make this quantitative comparison across 30 brown bear populations. Results from this study strongly supported the previous models and suggest that extensive home-range overlap will occur in areas with abundant and limited food sources, while more intermediate areas will have less overlap. McCutchen (1990) reported little overlap for female bears in RMNP. However, the reported sample size was for only 2 individuals; current research suggests that this degree of overlap may be somewhat higher (Baldwin 2008). Several investigators have noted non-territoriality among mammals when resources are patchy or limiting (e.g., Reynolds and Beecham 1980, Maher 1994, McLoughlin et al. 2000, Samson and Huot 2001). This would provide a likely explanation for the observed levels of home-range overlap in RMNP.

Seasonal differences in home-range size also exist and are primarily the result of 2 main factors. First, adult males and adult females have expanded home-ranges during the breeding season to optimize mating opportunities (Alt et al. 1980, Manville 1983, Rogers 1987), while females with young cubs use a compressed area until the cubs are able to travel greater distances (usually towards fall; Lindzey and Meslow 1977b, Alt et al. 1980, Hirsch et al. 1999). The other seasonal alteration in core-use areas is due to shifts in food abundance (Alt et al. 1980, Garshelis and Pelton 1981, Rogers 1987, Hellgren 1988, Beck 1991, Schwartz and Franzmann 1991, Samson and Huot 1998). These seasonal movements can cause problems for National Parks that control disturbances such as logging and fire (Bunting 1996, Hessl and Graumlich 2002). By eliminating such disturbances, habitats are allowed to progress towards successional climax with few early successional habitats available (Bender and Keller 2005). These early successional habitats are important food sources for black bears during summer and early fall (Poelker and

Hartwell 1973, Beeman and Pelton 1980, Garshelis and Pelton 1981, Rogers 1987, Hellgren et al. 1991, Schwartz and Franzmann 1991, Samson and Huot 1998, Mitchell and Powell 2003). While disturbances are limited in National Parks, they typically are not on adjoining property. Therefore, foods associated with disturbed sites (such as soft mast species) are available off National Parks, but these locations do not afford the protection that is available on park property. For example, Samson and Huot (1998) found that bears moved off La Mauricie National Park (LMNP), Québec, Canada, during summer and fall to forage on soft mast foods. Subsequent mortality associated with this shift in activity resulted in mortality rates that were close to the maximum sustainable mortality rate derived for LMNP (Samson and Huot 1998). This same situation could be problematic for bears in RMNP, as disturbance factors have been curtailed on RMNP resulting in little early successional habitat (McCutchen 1993, Bender and Keller 2005). Therefore, bears may be leaving the park in search of additional food sources. Some evidence exists for such mortality as hunting accounted for 2 of 3 known deaths of male bears monitored in RMNP from 1985–1991 (Zeigenfuss 2001). However, an assessment of the availability of critical habitats on the park should give a better understanding of if and how this lack of early successional habitat is affecting bear populations.

Activity patterns

One step toward delineating critical habitats occurs through an understanding of the activity patterns of bears. Of primary interest is how bears optimize time constraints on foraging, social activities, and environmental requirements (Aschoff 1964). Several different techniques have been used to assess activity patterns in bears including the movement and/or fluctuation of radio signals (Roth 1983, Roth and Huber 1986, Bjarvall and Sandegren 1987), motion sensitive collars (Garshelis and Pelton 1979, 1980, Garshelis et al. 1983, Larivière et al. 1994, Wagner et al. 2001), and direct observation (Jonkel and Cowan 1971, Herrero 1983, MacHutchon 2001). The movement of a radio signal relies on the observers ability to detect changes in the location of an emitted signal and therefore, is able to assess only 1 kind of activity (active or not). Because of this, intense foraging bouts that occur within a small area could go unnoticed, thus representing a bias (Wagner et al. 2001). Knowlton et al. (1968) provided further evidence suggesting that signal fluctuations were not an appropriate method for assessing activity.

Motion-sensitive collars have been used for many years to assess activity patterns and can be reliable for assessing activity budgets of black bears (e.g., Garshelis and Pelton 1979, Garshelis et al. 1982, Larivière et al. 1994). These collars can be used to determine the level of activity or simply to discern active vs. inactive individuals (Wagner et al. 2001). Motion-sensitive collars typically perform better than relying on movement or fluctuations in radio signals, but have problems including a need to calibrate the collar to known levels of activity (Wagner et al. 2001) and provide a lack of information on the specific activities of the bear at the time of recording (MacHutchon 2001).

Direct observation is the preferred method for assessing activity patterns as it allows the observer to directly assess activity budgets of individuals. However, it can be very difficult in cryptic species (such as black bears; McCutchen 1990, Larivière et al. 1994) as it requires continuous observation of individuals over an extended period of time (MacHutchon 2001). Nonetheless, direct observation is 1 of the only ways to assess specifically what a bear does and eats during a 24-hour period and is a valuable tool when assessing the activity budget of bears.

Black bears are typically solitary, as social interactions between black bears are usually limited to male and female contact during the breeding season, females and young, siblings after weaning, and at feeding sites (Herrero 1983, Pelton 2003, Rogers 1977). Their solitary existence appears to be the result of 2 main factors: 1) they have little need for group protection, and 2) their primary food sources (e.g., berries, insects, hard mast) are usually too scattered for group feeding (Rogers 1987). Therefore, there is no advantage to group living. However, dumps and other feeding stations provide the exception. In such areas of abundant food sources, bears tolerate the presence of other individuals (Herrero 1983, Rogers et al. 1976, Rogers 1987) and will occasionally engage in play activity with other conspecifics (Rogers 1987).

Black bears are typically crepuscular or diurnal, but time of activity also appears to be influenced by the kind and amount of foods present, breeding activity, and the presence or absence of humans (Amstrup and Beecham 1976, Ayres et al. 1986, Larivière et al. 1994, Lindzey and Meslow 1977b, Beckmann and Berger 2003b, Pelton 2003). Numerous investigators have noted differences in diel activity throughout and among years. Upon emergence from den sites, individuals generally remain inactive for a period of time, as food sources are not available (Rogers 1987). It is not known for sure why bears abandon dens prior to food source availability, but is believed to be related to energy conservation. In a study conducted in northeastern Minnesota, Rogers (1987) reported temperatures in dens to be below that of ambient air temperatures at the time of emergence (generally between late March and early April). Therefore, even if food sources were not available at the time of emergence, the use of solar radiation (sun bathing) while maintaining lower metabolic activity could make it energetically efficient for bears to exit dens.

Once vegetative green-up occurs, bear activities increase. A small peak in activity is typically seen during the breeding season (Hamilton and Marchinton 1980, Rogers 1987), while a larger peak is observed during late summer and early fall. This peak coincides with hard and soft mast production (Garshelis and Pelton 1980, Garshelis et al. 1983, Larivière et al. 1994, Pelton 2000). The length of time that bears remain active throughout the year appears to be influenced by the abundance of available foods. Abundant food sources existing late into the year may act to delay denning activities (Beecham et al. 1983, Hugie 1982, Johnson and Pelton 1980, Kolenosky and Strathearn 1987, Larivière et al. 1994, Schooley et al. 1994b, Tietje and Ruff 1980).

Numerous investigators have also noted shifts to more nocturnal habits when bears occur in close proximity to humans (e.g., Ayres et al. 1986, Herrero 1983, Reimchen 1998, Pelton 1999, Beckmann and Berger 2003a). Ayres et al. (1986) and Beckmann and Berger (2003a) noted that this shift coincided with the decline in human activity and is likely an adaptation to reduce interaction with humans. Current evidence from RMNP suggests that the resident population is behaving in the same manner (i.e., crepuscular to diurnal in more natural locations, crepuscular to nocturnal in heavy human-use areas; R. Baldwin, personal observation).

Hibernation and denning

Hibernation is a form of winter dormancy expressed among mammals and is an adaptation to cold environments that lack abundant food sources during this season (Watts et al. 1981, Ruby 2003). Denning provides shelter from inclement weather and predators, but hibernation is the mechanism that makes it energetically feasible to utilize dens (Beck 1991). In hibernators that experience deep torpor (body temperatures < 10°C), individuals typically reduce respiratory rates by 10–100 fold, decrease heart and metabolic rates, have a relaxed muscle tone, and maintain a curled-up position that conserves body heat (Folk et al. 1972, Lyman et al. 1982, Nelson et al. 2003). These deep hibernators will typically maintain body temperatures 1–3°C above ambient temperatures for a few days to several weeks at a time (Lyman et al. 1982), but then for reasons unknown, will spontaneously rewarm for short periods of time before reentering torpor (Ruby et al. 2002). Initial debate existed about classifying bears as true hibernators (e.g., "winter lethargy"; Hock 1960), as they do not exhibit deep torpor followed by periods of arousal. Rather, they maintain temperatures slightly below their euthermic norm (approximately 5 and 4°C below norm; Craighead et al. 1976, Rausch 1961, respectively) throughout the dormancy period (Folk et al. 1972, 1976, Nelson et al. 1983), thus maintaining skeletal muscle strength and activity for quick arousal during emergencies (Tinker et al. 1998, Harlow et al. 2001, Nelson et al. 2003). However, more recent investigations have determined that bears do share several additional characteristics with true hibernators (i.e., high serum magnesium, reduced QT interval of heartbeat; Folk et al. 1972, 1976), and may show a more profound and efficient form of hibernation than that exhibited by more classic hibernators (e.g., woodchucks [*Marmota monax*]; Folk 1967, Folk et al. 1972, 1976).

Unlike classic hibernators, bears do not have to consume food or water, nor do they need to urinate or defecate throughout the course of the dormancy period (Hock 1960, Folk et al. 1972, Nelson et al. 1983, Pelton 2003). Bears do not need to eat due to the accumulation of fat from late summer to late fall. This fat typically supplies all energy required during hibernation (Nelson et al. 1975, Lundberg et al. 1976), and catabolism of this fat provides metabolic water to replace that which is lost from respiration (Nelson et al. 1973). Urine is produced daily, but is reabsorbed through the bladder wall, thus maintaining urea concentrations (Nelson et al. 1975).

Uremia is avoided through a series of reactions. First, alanine is produced and in turn yields glucose. Then through transamination reactions, other amino acids are produced and enter protein synthetic pathways more readily in winter than in summer (Lundberg et al. 1976, Nelson et al. 1983). These reactions allow the bear to preserve muscle tissue and avoid uremia (Nelson 1980, Nelson et al. 1983). What little urea produced is metabolized and degraded (Nelson et al. 1975). These metabolic adaptations allow relatively quick arousal times for defense and care of themselves and young (Pelton 2003), while maintaining or increasing metabolic efficiency compared to “classic” hibernators (20–27% winter weight loss for black bears; 25–30% winter weight loss for “classic” hibernators [Hock 1960, Kayser 1961]). However, if fat supplies are depleted, protein catabolism will occur, resulting in a loss of lean body mass (and a corresponding total weight loss of 3–7%; Maxwell et al. 1988). This situation could lead to dehydration and may potentially be life threatening (Maxwell et al. 1988).

Hibernation is a necessary adaptation for survival of most North American bear populations, but appears to require a pre and post-hibernation period to adapt to the required biological adjustments (Lindzey and Meslow 1976b, Johnson and Pelton 1979, Hamilton and Marchinton 1980, Nelson et al. 1983, Pelton 2003). The pre-hibernation period may last up to 1 month and is likely a physiological and behavioral adaptation that allows the digestive system to prepare for hibernation (Nelson et al. 1983, Pelton 2003). Sometime during the pre-hibernation period, select vegetative material is consumed that acts as a fecal plug in the lower colon to prevent defecation during hibernation (Hamilton and Marchinton 1980). This plug is typically constituted of a random collection of vegetative materials, bear hair, and a residue of secretions (Smith 1946, Johnson and Pelton 1979). Following hibernation, this plug is excreted.

The transition back to normal metabolic rates occurs during post-hibernation (sometimes referred to as walking hibernation; Nelson et al. 1983). This period typically lasts for 10–14 days. During this time, bears become active but do not resume normal food or water consumption, even if readily available (Nelson et al. 1979, 1983). However, nitrogen loss through urine is negligible and daily excretions of calcium, phosphorous, and magnesium are low. Therefore, it appears that the biochemical stage of hibernation persists during the post-hibernation period, thus explaining the lack of food and water consumption during this time (Nelson et al. 1979, 1983).

Hibernation is the process that allows bears to survive through the winter season. However, dens are the structures that provide shelter and protection during this period (Beck 1991). Many types of dens are used (abandoned buildings and foundations [Skinner 1925, Jonkel and Cowan 1971]; ground [Hamilton and Marchinton 1980, Hellgren and Vaughn 1989, Wooding and Hardisky 1992, White et al. 2001, Martorello and Pelton 2003]; culvert [Barnes and Bray 1966]; excavated [Erickson et al. 1964, Tietje and Ruff 1980, Beecham et al. 1983, Hayes and Pelton 1994, Smith et al. 1994b]; rock cavity [LeCount 1983a, Beck 1991, Doan-Crider and Hellgren 1996, Zeigenfuss 2001]; snow den [Manville 1987]; tree dens [Johnson and Pelton 1981, Wathen et al. 1986, Weaver and Pelton 1994, Oli et al. 1997, Klezendorf et al. 2002]) and the selection of den type appears to be influenced by a combination of factors including den availability, potential thermal regulation, protection from predators, and protection from the environment.

In an attempt to reduce heat loss, bears often line dens with litter as energy expenditure is reduced if dens are well insulated (Lentz et al. 1983). This nesting material is particularly valuable as most heat is lost from conduction through the ground (Maxwell et al. 1988). This litter often includes pine boughs, leaf litter, moss, bark, and grass (Maxwell et al. 1972, Johnson and Pelton 1979, Tietje and Ruff 1980, Beck 1991, Smith et al. 1994b, Costello et al. 2001), and can range in depth from a few to 30 centimeters (Reynolds et al. 1976, Tietje and Ruff 1980, LeCount 1983a, Davis 1996, Bertram and Vivion 2002). However, in some locations, nesting materials are absent, likely a result of warmer temperatures or lack of availability of nesting materials at the time of denning (Erickson et al. 1964, Jonkel and Cowan 1971, Davis 1996).

In colder environments, den size may have an influence on den selection. Several investigators noted a relationship between body size and den size (Pearson 1975, Tietje and Ruff 1980, Bertram and Vivion 2002). They concluded that larger den chambers would facilitate greater heat loss, and therefore, were selected against. However, this appears to relate only to bears in the most northern extension of their range, as den sizes are quite variable in response to bear size in warmer locations (Beck 1991, Davis 1996).

Of the different den types, excavated and tree dens appear to provide the greatest thermoregulatory advantage. Most studies conducted in the northern-most parts of their range show bears using excavated dens (e.g., Tietje and Ruff 1980, Smith et al. 1994b, Bertram and Vivion 2002), presumably due to the greater insulative ability of soil vs. rock (Folk et al. 1972). Near Fairbanks, Alaska, Folk et al. (1972) reported that an unoccupied, excavated den maintained a temperature 37ºC higher than the ambient temperature, while in northeastern Minnesota, Rogers (1987) reported temperatures within closed dens to remain slightly below 0ºC even when external temperatures dropped as low as –41ºC. However, he noted that most dens in this area were open and resulted in temperatures only 1–2ºC warmer than ambient temperatures, but did still serve as efficient windbreaks.

In eastern localities, tree dens provide greater thermoregulatory protection and are selected for when available, particularly by females (Johnson et al. 1978, Pelton et al. 1980, Wathen et al. 1986, Weaver and Pelton 1994, White et al. 2001). Pelton et al. (1980) noted that this protection was due to the avoidance of 3 primary factors that affect the rate of heat loss and energy consumption: movement of cold air along the ground surface, insulation provided by forest canopy (decrease of cold winds above ground level), and a dry interior cavity. Specifically, Johnson et al. (1978) determined that using tree dens resulted in a > 15% energy savings vs. denning on the ground and yielded drier den sites (Johnson and Pelton 1981).

In addition to thermal advantages, tree dens also afford superior protection from human and environmental disturbance. Numerous investigators reported substantially reduced abandonment of tree dens compared to other den types when approached (i.e., Pelton et al. 1980, Weaver and Pelton 1994, Costello et al. 2001). This was likely due to the inaccessibility of the den to most potential predators (Costello et al. 2001). Utilization of above ground den locations is also important to cub survival in flood-prone areas, as seasonal floods can result in reproductive failure (Alt 1984, Smith 1985, Weaver and Pelton 1994, Oli et al. 1997, White et al. 2001).

Although rock dens may not be as energy efficient as excavated and tree dens, they do provide excellent protection from predators (i.e., wolves and other bears; Rogers and Mech 1981, Alt 1984, Horejsi et al. 1984, Tietje et al. 1986). Rock dens are typically located on steep slopes in well protected areas (Hayes and Pelton 1994, Costello et al. 2001, Zeigenfuss 2001). In addition, these dens typically have small openings that afford bears greater protection from predators when denning (median = 35 and 50 cm in west-central Colorado for females and males, respectively; Beck 1991). If a bear is disturbed in their den, they typically position themselves near the den entrance as it is the most defensible part of the den (Beck 1991, R. Baldwin, personal observation). Therefore, smaller den openings provide a significant advantage for defense. Most dens in RMNP are rock dens with little relationship between bear and den-chamber size (Zeigenfuss 2001, R. Baldwin, personal observation) suggesting that defense and protection may be more important than thermoregulatory aspects (Beck 1991).

In the absence of alternative den locations, bears may use ground dens (i.e., Johnson and Pelton 1981, Wooding and Hardisky 1992, Hayes and Pelton 1994, White et al. 2001). To account for decreased thermoregulatory insulation and increased predation risk, most ground dens are found surrounded by dense vegetation (LeCount 1983a, Kolenosky and Strathearn 1987, Hellgren and Vaughan 1989, Hayes and Pelton 1994, Martorello and Pelton 2003). It is unlikely that these den sites afford the same protection as other dens, as bears using ground dens have less protection from the environment and are more prone to disturbance by humans and other animals (Johnson and Pelton 1981, Weaver and Pelton 1994, Costello et al. 2001). However, it is unknown if this results in lower productivity in bears when compared to bears using other den types (Hellgren and Vaughan 1989, Hayes and Pelton 1994).

Time of den entrance and exit varies among populations and demographic makeup of populations. All black bear populations living in northern regions den (Linnell et al. 2000), but not all cohorts den in their southern expanse (e.g., Hamilton and Marchinton 1980, Hellgren and Vaughan 1987, Graber 1990, Doan-Crider and Hellgren 1996). However, even for southern populations, denning seems to be necessary for pregnant females, presumably for security of newborn cubs, and typically lasts for approximately 3 months (Graber 1990, Wooding and Hardisky 1992, Doan-Crider and Hellgren 1996). Generally, pregnant females spend the greatest time in dens, followed by non-pregnant females and subadult males. Adult males spend the least amount of time in dens with difference in time varying from a few weeks (e.g., Lindzey and Meslow 1976b, Beck 1991, Smith et al. 1994b) to months (e.g., LeCount 1983a).

Several ideas have been given to explain this difference in denning duration. A simple part of the answer is that female bears with cubs typically remain in dens longer due to the reduced mobility of young cubs (Lindzey and Meslow 1976b, Rogers 1987). However, other factors are likely involved. Several investigators believe that appropriate den selection is an important factor in cub survival (Johnson et al. 1978, Pelton et al. 1980, Tietje and Ruff 1980). They theorized that by denning earlier, they could select dens which provided the greatest protection (i.e., small openings that prohibit entrance of larger males) and were most energy efficient. Parturition and lactation have substantial effects on body weight (additional 9% weight loss [Tietje and Ruff 1980]; additional 37% fat loss [Harlow et al. 2002]). Therefore, dens that provide greater insulation should decrease the amount of body fat required for successful reproduction.

Related to this, Smith et al. (1994b) suggest that female black bears den when it no longer is energetically advantageous for them to remain active. Several investigators report a minimum body-condition threshold required to produce cubs (Rogers 1976, Alt 1989, Samson and Huot 1995). Therefore, in harsh climates, it may be advantageous for pregnant females to den soon after attaining such a level, as further activity may lead to a negative energy balance and result in a reduction of body condition to a level where reproduction is no longer possible (Schooley et al. 1994b).

Alternatively, Tietje and Ruff (1980) theorized that males could remain active for longer periods of time due to their decreased surface area-to-volume ratio. This decreased ratio would ensure less heat loss to the environment. A negative energy balance is unlikely to have as profound an impact on males as reproductive females as their energy requirements are not as great (Tietje and Ruff 1980, Schooley et al. 1994b)

Time spent in the den varies with latitude and elevation (7 months: Alaska [Schwartz et al. 1987, Bertram and Vivion 2002]; 6 months: Colorado [Beck 1991, Baldwin 2008]; 5 months: Arizona [LeCount 1983a]; 4 months: New York [O'Pezio et al. 1983], Michigan [Manville 1987]; 3 months: North Carolina [Hamilton and Marchinton 1980], Arkansas [Oli et al. 1997]) and has been attributed to a number of factors including snowfall (Jonkel and Cowan 1971, Northcott and Elsey 1971), temperature (Folk 1967, Lindzey and Meslow 1976b, Rogers 1987), precipitation (Hellgren and Vaughan 1989), photoperiod (Folk et al. 1976, Johnson and Pelton 1980, Nelson et al. 1983), food availability (Johnson and Pelton 1980, Tietje and Ruff 1980, Beecham et al. 1983, Schooley et al. 1994b), physical condition (Erickson and Youatt 1961, Carpenter 1973, Lindzey and Meslow 1976b, Schwartz et al. 1987), or some combination of these factors (Lindzey and Meslow 1976b, Johnson and Pelton 1980, Novick et al. 1981, Rogers 1987, Schooley et al. 1994b).

It is likely that the initial cue for denning is the reduction in photoperiod and temperature associated with late autumn and early winter (Johnson and Pelton 1980, Schooley et al. 1994b). However, the overriding factor influencing denning dates may actually be the present energy balance of the bear (Lindzey and Meslow 1976b, Elowe 1984, Smith 1985, Schooley et al. 1994b). If food is abundant, the bear is likely to continue foraging. Once a negative energy balance occurs, it will no longer be advantageous for them to continue foraging. At this time, the bear will enter their den.

In most expanses of the black bears range, food availability is likely the best indicator of the denning period. In captive bears, Erickson and Youatt (1961) reported that when bears were fed, they remained active. However, when feeding was halted, denning promptly occurred. Several other studies have reported extended foraging periods during years of heavy mast production (Johnson and Pelton 1980, Tietje and Ruff 1980, Hugie 1982, Beecham et al. 1983, Schooley et al. 1994b, Costello et al. 2001). Therefore, food availability appears to be the proximate factor influencing the date of den entrance.

However, other factors are related to energy balance as well. Weather can affect food availability by influencing the abundance, timing, and quality of food items (Schooley et al. 1994b). If heavy snowfall is present, food sources will be difficult to acquire. Therefore, even if abundant food sources are present, a negative energy balance will occur due to the difficulty associated with food acquisition. Likewise, colder temperatures and rainfall can increase the amount of energy required to forage and will have an impact on their energy balance. Therefore, modeling den entrance dates would likely involve a balance between food abundance and other secondary factors.

Like den entrance, emergence appears to be influenced by several factors (cub development [Doan-Crider and Hellgren 1996]; photoperiod [Lindzey and Meslow 1976b, Kolenosky and Strathearn 1987]; snow melt [Rogers 1987, Schoen et al. 1987, Schwartz et al. 1987]; spring precipitation resulting in den flooding [Oli et al. 1997]; spring temperatures [Lindzey and Meslow 1976b, O’Pezio et al. 1983, Kolenosky and Strathearn 1987, Rogers 1987]; vegetative green-up [Pearson 1975, Beck 1991, Schooley et al. 1994b]). It is likely that a combination of these factors affect den emergence, but an understanding of this interaction is lacking.

Food habits

The diet of black bears is highly varied, ranging from sedges and berries to insects and carrion. By definition, black bears are omnivores, but approximately 85% of their diet is vegetative material. What little animal matter consumed is generally made up of colonial insects (Hatler 1972, Clapp 1990, Pelton 2003), although they do have the ability to capture and consume live prey such as beaver (*Castor canadensis*), white-tailed deer fawns (*Odocoileus virginianus*), and moose calves (*Alces alces*; Franzmann and Schwartz 1986, Matthews and Porter 1988, Smith et al. 1994a). However, their diet varies considerably seasonally and regionally. When bears emerge from their dens, they typically enter into a period of negative foraging where they may consume small quantities of food, but generally continue to lose weight, due in part to reduced consumption but also due to the low nutritive value of available foods (Jonkel and Cowan 1971, Poelker and Hartwell 1973, Rogers 1976, Beeman and Pelton 1980, Eagle and Pelton 1983, Herrero 2002, Pelton 2003). Initial foods consumed include the previous year's hard and soft mast, carrion, and new plant growth (Kendall 1983, Irwin and Hammond 1985, MacHutchon 1989, Raine and Kansas 1990, Schwartz and Franzmann 1991, Costello 1992, Kasbohm et al. 1995). As spring progresses, bears spend more time foraging, usually on herbaceous material, such as sedges, squaw root, and horsetail (Hatler 1972, Graber 1983, Garner 1986, Hellgren and Vaughan 1988, Stubblefield 1993, Kasbohm et al. 1995, Payne et al. 1998). Summer feeding is characterized by a shift to soft mast and insects (Bennett et al. 1943, Hellgren and Vaughan 1988, MacHutchon 1989, Raine and Kansas 1990, Costello 1992, Hellgren 1993, Kasbohm et al. 1995, Roof 1997, Payne et al. 1998). During this time, bears are generally able to recoup some of the weight they lost over winter. The fall season is marked by a voracious appetite by black bears as they try to rapidly gain weight for winter dormancy. In many parts of their range, this means heavy consumption of hard mast species (i.e., acorns, beech and pine nuts; Bennett et al. 1943, Landers et al. 1979, Eagle and Pelton 1983, Graber 1983, Garner 1986, Hellgren and Vaughan 1988, Costello 1992, Roof 1997). However, where such foods are unavailable, foraging focuses on fall berries and insects (Hatler 1972, Poelker and Hartwell 1973, Rogers 1977, Irwin and Hammond 1985, MacHutchon 1989, Raine and Kansas 1990, Schwartz and Franzmann 1991, Kasbohm et al. 1995). During the summer or fall period, bears may travel great distances to utilize available food sources (Jonkel and Cowan 1971, Rogers 1987, Elowe and Dodge 1989, Schwartz and Franzmann 1991). However, they typically return to their normal spring and summer range for denning (Garshelis and Pelton 1980, Schooley et al. 1994a).

Consumption of human foods can be a problem in many areas, as these food sources are generally high in fat and protein (an aspect of bear diets that are generally lacking) and are easily obtained (Pelton 2003). In fact, high protein diets have been shown to be related to increased weight gains and fecundity in black bears, suggesting the importance of such foods in bear diets (Tate and Pelton 1983, Rogers 1987, McLean and Pelton 1990, Beckmann and Berger 2003a). Unfortunately, the utilization of human foods often brings bears into direct contact with humans and ultimately leads to conflicts (Harms 1980, Singer and Bratton 1980, Zardus and Parsons 1980, Herrero 2002, Beckmann and Berger 2003b). Tate and Pelton (1983) reported 624 aggressive actions by panhandling bears in Great Smoky Mountain National Park with 6% of these aggressive acts leading to actual physical contact with humans. In the Sierra Nevada-Great Basin interface, Beckmann and Berger (2003b) found that increased abundance of human foods led to a rapid shift of wildland bears to urban areas, a heavily skewed sex ratio towards males, changes in female reproductive success, an increase in body mass, and a reduction in home-range size, time spent foraging, and time spent in dens. Therefore, care must be taken to secure human foods from bears to minimize conflicts.

As with almost all black bear studies, vegetative material was the primary source of food historically for bears in RMNP, with berries (primarily *Vaccinium, Fragaria, Prunus, Shepherdia,* and *Rubus* spp.) and horsetail (*Equisetum* spp.) the most frequently occurring items (Zeigenfuss 2001). However, diets of black bears in RMNP differ from most populations in their frequent use of animal matter. Zeigenfuss (2001) reported > 40% of bear diets was comprised of arthropod parts, while > 13% was comprised of vertebrate matter. These numbers are somewhat unclear, as she defines diet composition based on percent scat composition. However, the percentages result in a value much greater than 100%. Nonetheless, it is apparent that bears in RMNP are using animal matter (particularly insects) at high rates.

Unfortunately, no dates were available for analysis of this data set and no nutritional data were obtained, so no seasonal description of food habits or nutritional information was available. Nonetheless, young vegetative growth (usually in the form of sedges, grasses, catkins, herbaceous material) is usually the predominant food source in early spring and is high in crude protein but also high in dietary fiber. Therefore, much of the vegetation is indigestible, usually leading to weight loss in early spring (negative foraging period; Eagle and Pelton 1983), although several investigators theorized that the weight loss might more accurately reflect a period of hypophagia than increased fiber content (Nelson et al. 1983, Hellgren et al. 1989).

During summer, bears consume greater quantities of soft mast and insects. During this time, the mean crude protein and crude fiber contents of foods typically decrease (Eagle and Pelton 1983). The shift to less fibrous materials results in higher protein and energy consumption. In particular, a few investigations have found a high use of ants in mid-summer

(48% scat composition at Banff National Park, Raine and Kansas 1990; 58% scat volume in north-central Minnesota, Noyce et al. 1997; female black bear spent three quarters of her time foraging for ants, Rogers 1976) and have speculated that this increased utilization coincided with increased abundance and size of ant broods and a decrease in forage quality of other available foods (especially protein; Noyce et al. 1997). Alternative sources of protein can be particularly important during mid-summer months, as protein content of vegetation decreases over time (i.e., with phonological development; Eagle and Pelton 1983, Noyce et al. 1997, Mattson 2001). Diets containing < 12–35% crude protein require increased energy metabolism (Rode and Robbins 2000). Therefore, energy requirements would be substantially higher if insufficient levels of protein were available.

Ants can also provide an important source of energy (Noyce et al. 1997, Swenson et al. 1999, Mattson 2001). In fact, a single ant mound can provide 230 kJ of digested energy (Swenson et al. 1999), thus constituting a major portion of a bears diet (mean daily maintenance cost approximately 700 kJ for a 70 kg bear subsisting on a diet that contains 35% crude protein; Rode and Robbins 2000). Therefore, higher insect consumption during mid-summer could be a function of both an increased need for protein and the availability of a high energy food source, or simply may represent the best available food source.

During autumn, where hard mast food sources are available, there is typically a shift to such items (see Clark 2004 for review). This shift results in lower protein intake but higher fat and energy intake (Eagle and Pelton 1983, Kasbohm et al. 1995). It is theorized that this shift allows for accumulation of fat for hibernation at the expense of increased lean muscle mass (Brody and Pelton 1988). This is possible because muscle mass lost during hibernation is replaced during the spring and summer months, allowing the bear to focus solely on fat accretion during autumn (Nelson et al. 1983, Brody and Pelton 1988).

In areas where hard mast is unavailable, the primary food sources are berries and insects. However, the results are approximately the same. Kasbohm et al. (1995) investigated the effects of a gypsy moth infestation on food habits and nutrition of black bears in Shenandoah National Park, Virginia. This infestation resulted in a complete loss of the acorn crop, causing a shift in dietary preference to soft mast, as soft mast crops increased due to canopy removal. This increased soft mast consumption combined with increased animal matter intake allowed for similar crude protein and fat intake when compared to pre-defoliation levels. Therefore, bears may be able to compensate for these changes by using a number of food sources though an increase in the time spent foraging would likely be required to offset the loss of higher energy food items.

One possible explanation for the increased fat intake may be related to a shift in digestibility that allows for a higher assimilation of high carbohydrate and fat foods at the expense of protein. Brody and Pelton (1988) showed that bears increase their ability to assimilate such compounds, and inferred that this may be a hormonally controlled adaptation that allows for rapid fat assimilation. High levels of protein would no longer be required, as lean body growth ceases in fall (Nelson et al. 1983). Such an adaptation would seem to provide a significant advantage for fat accumulation.

An understanding of how and why bears select foods is a necessary step towards understanding how they select habitats (Kansas and Raine 1990, Noyce and Coy 1990, Clark et al. 1994, Costello and Sage 1994). In addition, reproductive rates are related to nutritional availability (Jonkel and Cowan 1971, Rogers 1976, 1987, Eiler et al. 1989, Elowe and Dodge

1989, McLaughlin et al. 1994, Costello et al. 2003), which in turn is related to food availability. Most food habit studies have been conducted through scat or stomach analyses. Identification of food sources from stomachs requires dead individuals and, therefore, is not always possible. Scat analysis does not have this problem. Most scat analyses have assessed percent frequency and percent volume of ingested foods (i.e., Bennett et al. 1943, Hellgren and Vaughan 1988, MacHutchon 1989, Clapp 1990). Unfortunately, this only accounts for what is excreted by the animal; it does not specifically relate to what is ingested. However, Hewitt and Robbins (1996) developed correction factors to eliminate this bias that should be useful in further investigations.

An understanding of the quantity of different foods ingested is an initial step toward understanding the influence of food on reproductive rates and habitat selection. However, this information does not fully explain how these factors are influenced by nutrition. Nutritional information related to ingested foods and those available are needed to adequately assess this relationship (Gluesing and Field 1986). Several investigations have attempted to assess this relationship (Mealey 1975, Bunnell and Hamilton 1983, Eagle and Pelton 1983, Brody and Pelton 1988, Elowe and Dodge 1989, Hellgren et al. 1989, Kasbohm et al. 1995, Noyce et al. 1997, Welch et al. 1997, Rode and Robbins 2000). However, these studies were based on nutritional factors obtained for foods available and/or consumed but did not account for different levels of digestibility of foods (e.g., Kasbohm et al. 1995, Inman and Pelton 2002; but see Welch et al. 1997, Rode and Robbins 2000). Pritchard and Robbins (1990) have developed digestive and metabolic efficiencies for different bear foods. Application of these models to foods consumed should give a better understanding of how bears are selecting food sources (e.g., Welch et al. 1997, Rode and Robbins 2000). Subsequently, relationships between these nutritional levels and associated body condition measurements should elucidate which habitats are most important for bear survival and reproduction.

An alternative method for assessing food habits is through focal animal observation. This method relies on the ability of the observer to follow an individual for a selected period of time while recording activities of the subject (Morrison et al. 1992, MacDonald et al. 2000). Advantages of this technique include direct knowledge of what each individual animal consumes (i.e., allows observer to assess food habits for sex and age categories; not usually possible with scat analysis) and how much time it spends foraging on food items. It also allows for recording of exact locations as opposed to relative locations determined through triangulation. However, this technique relies on the assumption that the observer does not disturb the animal in any way (Rogers 1977). Also, measures of independence are difficult to determine (i.e., are measurements recorded in 2 hour intervals independent, are 2 day intervals independent, etc.; Morrison et al. 1992, MacDonald et al. 2000).

Observational studies on wild bears are relatively uncommon, due in part to their cryptic behavior (McCutchen 1990, Larivière et al. 1994, Pelton 2003). Most observational studies have been conducted on bears at garbage sites or along roadsides (e.g., Barnes 1967, Rogers et al. 1976, Herrero 1983). However, several investigators have been able to address various questions about bears through direct observation including food habits, habitat selection, and the effects of food supply and kinship on social behavior, population growth, and movements of bears (Rogers 1987, Rogers and Wilker 1987, Rogers et al. 1988, Mollohan et al. 1989, DeBruyn 1992, Bull et al. 2001, MacHutchon 2001) and suggest that focal animal sampling may provide additional information not obtainable through scat analysis. Such information should be useful in assessing food and habitat preferences of black bears.

Body condition

Knowing what and how much of certain food items bears consume, along with their associated nutritional compositions, are initial steps toward understanding their importance in bear energetics. For example, numerous studies have shown effects of food availability on habitat selection and reproductive success (e.g., Rogers 1977, Clark et al. 1994, Costello et al. 1994) as well as an association between body weight and reproductive success (e.g., Rogers 1976, 1987, McLean and Pelton 1990, Stringham 1990). However, nutritional quality should not be directly inferred from food availability (Pritchard and Robbins 1990), nor is body weight a direct measurement of body condition (Farley and Robbins 1994, Chan-McLeod et al. 1995, Gau and Case 1999). Therefore, the relationship between food availability, nutrition, and body condition should result in a better understanding of the interaction between these aspects and habitat selection and reproductive success (Hellgren et al. 1993).

Body condition is most often defined by either the percent of body mass that is fat or by the fat:nonfat ratio (Noyce et al. 2002). Determination of body composition and thus body condition is most accurately determined through chemical analysis of the entire carcass (Cattet et al. 2002). However, this is often cost prohibitive and requires that bears be dead. Therefore, many different techniques have been developed to estimate body condition in various mammals including bioelectrical impedance analysis (BIA; Farley and Robbins 1994, Atkinson and Ramsay 1995, Hilderbrand et al. 1998, Gau and Case 1999, Hilderbrand et al. 2000, Partridge et al. 2001, Gau and Case 2002, Noyce et al. 2002), isotopic water dilution (Arnould and Ramsay 1994, Farley and Robbins 1994, Atkinson and Ramsay 1995, Atkinson et al. 1996, Hilderbrand et al. 1998, 2000, Partridge et al. 2001), body mass and morphometric measurements (Schroeder 1987, Hellgren et al. 1989, Cattet 1990, Scott 1991, Noyce and Garshelis 1994, Samson and

Huot 1995, Cattet et al. 2002), ultrasonography (Stephenson et al. 1998, Cook et al. 2001, Stephenson et al. 2002), blood chemistry (Franzmann and Schwartz 1988, Hellgren et al. 1989, 1990, DelGiudice 1991, Hellgren et al. 1993, Noyce and Garshelis 1994, Gau and Case 1999, 2002), bone prominence and skin-fold measurements (Cook et al. 2001, Noyce et al. 2002), and internal fat levels (Cattet 1990, Scott 1991, LaJeunesse and Peterson 1993, Chan-McLeod et al. 1995, Stephenson et al. 1998, Cook et al. 2001, Stephenson et al. 2002). The following paragraphs provide a brief description of the techniques as well as their prior use and applicability for bears.

BIA.—Farley and Robbins (1994) developed protocols and equations to allow users to determine percent body fat in bears using BIA. During analysis, resistance to conduction is determined by passing a low-level alternating current through the body (Kushner 1992, Gales et al. 1994). This resistance value is related to body mass and snout-to-tail length to determine total body water. Determination of total body water is possible because conductivity of body lipids is 4–5% that of lean tissue, body fluids, and bone (Farley and Robbins 1994, Gau and Case 1999). Body lipid content can then be calculated using total body water, as the composition of fat-free mass is constant (Johnson and Farrel 1988, Robbins 1993, Gau and Case 1999). Farley and Robbins (1994) concluded that this technique is a rapid (5–15 minutes; Noyce et al. 2002), non-invasive, and highly accurate method (R^2 = 0.96, SEE = 2.2% [Farley and Robbins 1994]; R^2 = 0.88, SEE = 3.3% [Hilderbrand et al. 1998]) for estimating percent body fat and has since been validated by Hilderbrand et al. (1998) in a single blind study. However, this technique is sensitive to bear body position, mass and length measurements, previous injuries in the conductor path, and moisture on the fur when in direct contact with the ground (Farley and

Robbins 1994, Hilderbrand et al. 1998). Care must be taken to standardize protocols when using BIA.

Isotopic water dilution.—As with BIA, isotopic dilution measures total body water and relies on the close inverse relationship between water and fat and the constancy of protein and ash to fat-free mass (Robbins 1993, Farley and Robbins 1994). For this analysis, anesthetized bears are injected with either tritium or deuterium oxide and allowed to rest for > 120 minutes to allow equilibration of the isotope in the body water pool (Farley and Robbins 1994, Hilderbrand et al. 1998). After the required time, a blood sample is taken and serum extracted from centrifuged blood to allow analysis of tritium or deuterium content in blood. Total body water is then estimated as the ratio of the amount of isotope injected to the concentration measured after the equilibration time (Farley and Robbins 1994). This total body water measurement is then used in a predictive equation derived by Farley and Robbins (1994) to estimate percent body fat.

Isotopic water dilution is highly accurate in assessing percent body fat ($R^2 = 0.93$; SEE = 2.7% [Farley and Robbins 1994]; $R^2 = 0.94$, SEE = 2.3% [Hilderbrand et al. 1998]) and does not suffer from measurement error concerns of BIA. However, a major problem with isotopic water dilution is its lack of applicability in a field setting. This technique requires use of lab equipment and long sedation times, making it a more suitable technique for the lab (Farley and Robbins 1994, Hilderbrand et al. 1998). Interestingly, a combination of BIA and isotopic dilution appears to be the most accurate method for estimating body condition ($R^2 = 0.97$; SEE = 1.7% [Hilderbrand et al. 1998]). However, as with isotopic dilution, field application is difficult.

Body mass and morphometric measurements.—Body mass and associated morphometric measurements have served as surrogates of body condition for many years. Numerous reproductive parameters have been related to body mass (age of first reproduction [Rogers 1976, Beecham 1980, Noyce and Garshelis 1994]; litter size [Alt 1989, Samson and Huot 1995]; sex ratios [Noyce and Garshelis 1994, Samson and Huot 1995]) and various morphometric measurements have been developed to provide a more universal approach to estimating body condition across different populations (e.g., length/weight ratios; Schroeder 1987, Hellgren et al. 1989). Certainly many associations derived from body mass measurements are simple to apply and informative across broad scales, but they lack the ability to define body condition at the resolution required for exact applications (i.e., analysis of energy balance, survival rates, habitat selection, productivity parameters) due to the variation in shapes and sizes across different demographic parameters (i.e., age, sex, locality, body composition; Berg and Butterfield 1976, Calder 1984, Swenson et al. 1987, Atkinson et al. 1995, Hilderbrand et al. 2000).

To account for this inherent weakness, models using morphometric measurements were developed. Initially, simple length/weight ratios were employed (Schroeder 1987, Hellgren et al. 1989). However, these ratios were inadequate, as the developed ratios were correlated to age and nonfat body weight (Hellgren et al. 1989, Cattet 1990). Multivariate models were constructed to eliminate this relationship. Cattet (1990) and Scott (1991) developed such models in an attempt to determine body condition in bears. They were able to accurately predict nonfat body weight in black bears (straight-line body length [cm], age [years], and foreleg circumference [cm]: $R^2 = 0.985$ [Cattet 1990]; forearm circumference [cm], neck circumference [cm], head width [cm]: $R^2 = 0.890$ [Scott 1991]). However, determination of percent body fat was tenuous at best, and only useful for comparisons between groups rather than for individuals due to the large variation observed between predicted and observed fat mass (Cattet 1990, Scott 1991).

Although multivariate models were much better than simple length/weight ratios, they were limited by variations within sex, age, reproductive state, geographical population, and date at time of measurement (Cattet et al. 2002). Therefore, Cattet et al. (2002) developed models using residuals from the regression of mass against straight-line body length. These developed models exhibited a strong relationship between estimated body condition and true body condition (polar, black, and grizzly bears: $r = 1.00$) and resulted in highly significant models (polar bears: $R^2 = 0.98$; black bears: [$R^2 = 0.93$]). Nonetheless, measurement error is an inherent flaw that exists with all body condition indices derived from morphometric measurements (Eason et al. 1996, Cattet et al. 1997, 2002, Noyce et al. 2002). This error can be minimized by utilizing few observers and developing stringent standards for data collection (Eason et al. 1996, Noyce et al. 2002).

Bone prominence and skin-fold thickness are alternative indices for assessing body condition in various species (sheep [*Ovis aires*], Russel et al. 1969; dairy cattle [*Bos taurus*], Otto et al. 1991; caribou [*Rangifer tarandus*], Gerhart et al. 1996) and appear to be applicable in bears, as well. Noyce et al. (2002) compared such measurements to percent body fat derived from BIA and determined that they were as good or better than body mass at determining certain reproductive parameters. They determined that such techniques would be beneficial to employ, as BIA is expensive and not without sources of error. Nonetheless, BIA was more accurate estimating body condition and should be used where great accuracy is required.

Ultrasonography.—The use of ultrasonography to measure fat and muscle depth at specific points on the body (usually along rump or scapular region; Stephenson et al. 1998, Cook et al. 2001) is an efficient technique for estimating body condition in various species (moose, Stephenson et al. 1998; elk, Cook et al. 2001; mule deer [*Odocoileus hemionus*], Stephenson et al. 2002). To derive predictive equations, fat and/or muscle depth was measured using electronic calipers with resulting depth measurements related to actual fat and lean body mass estimates derived from chemical analysis of the carcass (Stephenson et al. 1998, Cook et al. 2001, Stephenson et al. 2002). Resulting equations have been fairly efficient at estimating percent body fat ($R^2 = 0.80$, Stephenson et al. 1998; $R^2 = 0.90$, Cook et al. 2001; $R^2 = 0.83$, Stephenson et al. 2002), but are unable to measure fat depth below certain minimum levels (e.g., ~ 5.6% for mule deer; Stephenson et al. 2002). Nonetheless, this technique has been effective in determining body condition in several ungulate species and could be applicable in bears, as well.

Blood chemistry.—Several studies have shown a relationship between various blood parameters and body condition of bears (Schroeder 1987, Franzmann and Schwartz 1988, Hellgren et al. 1989, DelGiudice et al. 1991, Hellgren et al. 1993). To determine this relationship, the investigators compared various blood profiles to another measure of body condition. Initially, various measures of body size (primarily body weight) were used as the comparative measure. These studies showed a relationship between hemoglobin and packed cell volume to body condition (Schroeder 1987, Franzmann and Schwartz 1988, Hellgren et al. 1989, DelGiudice et al. 1991, Hellgren et al. 1993; but see Noyce and Garshelis 1994). However, it was suggested that these results only provided crude estimates of body condition, and thus, were applicable only as population-wide estimators (Franzmann and Schwartz 1988, Noyce and Garshelis 1994). Later, Gau and Case (1999, 2002) related blood characteristics to body condition estimates derived from BIA. They found no correlation between any blood parameters and body condition. The observed difference in results is likely due to the difference in body condition measurements used. Additionally, using blood chemistry to define condition with short-term data often varies too much to be useful. BIA is considered a superior method for estimating body condition in bears (Farley and Robbins 1994, Hilderbrand et al. 1998), suggesting that results obtained from earlier investigations are limited at best. Presently, blood chemistry does not appear to be a viable method for estimating body condition of bears.

Internal fat levels.—Levels of fat in bone marrow, muscle, and around the kidney have been used to assess body condition in various species and have yielded moderate success (e.g., $R^2 = 0.41–0.78$ and $R^2 = 0.61–0.72$ for femur marrow fat and left kidney fat, respectively, in caribou; Chan-McLeod et al. 1995). However, some of the models have resulted in a curvilinear relationship (e.g., LaJeunesse and Peterson 1993), which is considered unsuitable for predictive purposes (Robbins 1993). In bears, Cattet (1990) assessed the relationship between body condition and fat in bone marrow and muscle, while Scott (1991) attempted to determine body condition using fat around the kidney and in bone marrow. Results from these investigations showed little promise for the use of these techniques in bears. Regardless, even if efficient and appropriate, this technique is of limited value as it is not applicable to live bears.

Habitat selection

Prime black bear habitat is typically defined by relatively inaccessible terrain, abundant food sources, and thick understory vegetation (Pelton 2003). However, regional variation exists in specific habitat components. In the southeast, there are 2 primary habitat types: mountains and coastal plain. Prime mountain habitats typically occur in relatively steep terrain covered by either oak-hickory (*Quercus-Carya*) or mixed mesophytic forests. Understory vegetation includes berry producing plants such as blueberry (*Vaccinium* spp.), blackberry (*Rubus* spp.), and raspberry (*Rubus* spp.), with laurel (*Kalmia latifolia*) and rhododendron (*Rhododendron* spp.) providing thick understory cover. Coastal plain habitats are low elevation areas with black gum (*Nyssa sylvatica*) and cypress (*Taxodium* spp.) as dominant overstory vegetation in mesic areas and pine (*Pinus* spp.) and oak dominant in drier areas. Greenbrier (*Smilax* spp.), holly (*Ilex* spp.), huckleberry (*Gaylussacia* spp.), and arrow-arum (*Peltandra virginica*) are typical understory plants that provide food and cover (Pelton 2003).

In the northeast and upper Great Lakes region, overstory hardwood species include beech (*Fagus* spp.), birch (*Betula* spp.), and maple (*Acer* spp.), with spruce (*Picea* spp.) and balsam fir (*Abies balsamea*) comprising the main coniferous component in prime bear habitat. However, swampy areas are primarily composed of northern white-cedar (*Thuja occidentalis*). Important food sources include blueberries, raspberries, apples (*Malus* spp.) from abandoned orchards, corn (from agricultural areas), and oak-hickory mast (Hugie 1974), with swamp vegetation providing excellent cover (Pelton 2003).

Along the Pacific coast, forest canopy in prime bear habitat is dominated by redwood (*Sequoia sempervirens*), hemlocks (*Tsuga* spp.), and Sitka spruce (*Picea sitchensis*). Drier sites commonly include lodgepole pine (*Pinus contorta*), ponderosa pine (*Pinus ponderosa*), and Douglas-fir (*Pseudotsuga menziesii*), with early successional areas such as brushfields, wet and dry meadows, high tidelands, riparian areas, and a variety of mast-producing hardwood species important for food and cover (Lawrence 1979, Pelton 2003). In the southwest, bears are primarily found in vegetated mountainous areas from 900–3,000 m in elevation. Oak and pinyon-juniper (*Pinus-Juniperus*) woodlands are the primary habitats, although bears occasionally move into open areas to feed on prickly pear (*Opuntia* spp.) (Waddell 1979, Pelton 2003).

Spruce-fir and lodgepole pine forests dominate much of the habitat occupied by bears in the Rocky Mountains. Important food sources include various berry producing plants (i.e., whortleberry [*Vaccinium* spp.], bearberry [*Arctostaphylos uva-ursi*], raspberries), with whortleberry and bearberry dominating much of the understory (McCutchen 1990). Heavily used nonforested areas include avalanche chutes, roadsides, burns, wet meadows, riparian areas, sidehill parks, and subalpine ridgetops (Kemp 1979, Pelton 2003). In RMNP, historically, bears follow this same general pattern with females preferentially selecting lodgepole and spruce-fir habitats while males preferred lodgepole habitats (Zeigenfuss 2001).

Bears shift habitat utilization patterns depending on the season. Rogers et al. (1988) noted that bears in Minnesota used primarily wetland areas with abundant new growth in early spring, while in Arkansas, Clapp (1990) reported heavy use of oak-dominated forests where leftover acorn mast was consumed during early spring. In late summer and early fall, black bears sometimes move long distances to utilize abundant food sources associated with these distinct habitats (Rogers 1987, Elowe and Dodge 1989, Schwartz and Franzmann 1991, Clark 2004) but return to prior sites before denning (Garshelis and Pelton 1980, Schooley et al. 1994a).

The selection of habitats by bears appears to be affected by several basic requirements including food, water, denning locations, escape cover, and movement corridors (Rogers 1993, Pelton 2000). Food availability may be the overriding factor influencing bear habitat selection (Rogers 1993). Quantity and quality of food affects survival and reproduction (discussed at length in prior sections). In addition, presence of abundant food patches appears to influence overlap of bear home-ranges (Powell 1987, Samson and Huot 2001). In areas where food is either extremely abundant or extremely scarce, it is not energetically viable to defend territories (Brown 1964, Krebs and Davies 1993, Samson and Huot 2001), but when food abundance falls somewhere in between, semi-exclusive home-ranges may be maintained (e.g., Jonkel and Cowan 1971, Hugie 1982, Young and Ruff 1982, Pelchat and Ruff 1986, Rogers 1987). However, even in such situations, some overlap often occurs (e.g., Amstrup and Beecham 1976, Powell 1987, Horner and Powell 1990) likely due to the co-utilization of abundant food patches (Samson and Huot 2001).

Many indirect effects of food availability on habitat selection also exist. Lack of food can cause malnourishment, subsequently weakening cubs and leaving them susceptible to predation and disease (Jonkel and Cowan 1971, Rogers and Rogers 1976, Rogers 1987, Pelton 1989, Rogers 1993). Likewise, food scarcity can lead to increased movements resulting in unusual social encounters (Schorger 1949, Rogers 1987) and increased human-related mortality (vehicular collisions, hunting, nuisance control; Rogers 1976, 1987, Kane 1989, Pelton 1989, McDonald et al. 1994, Clark 2004). Even in the absence of food scarcity, supplemental sources can have a significant impact on “habitat” selection, as the abundance of anthropogenic food sources can greatly alter behaviors of black bears (Herrero 1983, Rogers 1987, Beckmann and Berger 2003a).

Interestingly, black bears can maintain populations even where food productivity is low due to their ability to grow slowly. However, in these situations, mortality rates must be minimized to assure population viability, as corresponding reproductive rates are low. Rogers (1993) noted that bears historically occupied most areas ranging from Mexico and Florida north to treeline. He argued that black bear existence in low productivity areas meant that food supplies can *limit* bear populations but do not work in a density-dependent manner to *regulate*. However, food supply more likely serves as a *regulatory* factor, as food failures can lead to reproductive failure and high mortality (Pelton 1989).

Water must be readily available throughout the year for bears to utilize areas in an unrestricted manner (Hugie 1979). Wetlands and riparian areas are used for thermoregulation (i.e., wallowing; Kelleyhouse 1980, Rogers and Allen 1987) and foraging on hot days, as heat stress can limit use of open areas on hot days (Jonkel and Cowan 1971, Rogers 1980, Rogers and Allen 1987). Although water is required while consuming nuts, insects, and vegetation, it is not needed in great quantities while consuming berries (Rogers and Allen 1987). Precipitation may result in the greatest influence of water on habitat selection. In areas with insufficient rainfall, food abundance will not be great enough to support bears (Rogers 1993). Therefore, in contrast to food supply, water may *limit* populations, but does not likely *regulate* them (Rogers 1993).

Denning may be the most vulnerable time in a bear’s life-cycle (Pelton 2000). Therefore, habitat selection must include appropriate denning sites. In northern localities, excavated dens or thick vegetation combined with the presence of snow may adequately provide appropriate den sites (Erickson et al. 1964, Tietje and Ruff 1980, Rogers 1987). However, in more southern localities, reproductive success is highest for females where tree dens are present (Johnson and Pelton 1981, White et al. 2001). Therefore, habitats with available tree cavities may be selected by females though males will use a number of potential den types (Johnson and Pelton 1981, Wathen et al. 1986, Costello et al. 2001). In general, fewer disturbances occur when denning in more secure locations (i.e., thick vegetation, high in tree, deep in crevice; Pelton et al. 1980, Hayes and Pelton 1994, Pelton 2000). Some evidence suggests that den sites are limiting factors in bear population size (Weaver and Pelton 1994, Oli et al. 1997). Nonetheless, it appears that den sites will only act as a density-dependent factor if the abundance of appropriate den locations is limited (Rogers 1993).

Large trees and thick vegetation provide bears with security cover (Rogers 1993, Pelton 2000). These aspects are particularly important in heavy human-use areas and where other bear encounters area frequent. Large trees (> 50 cm dbh) are important for escape routes of cubs and for black bear encounters with humans and grizzly bears (Rogers 1993), as grizzlies can predate on black bears when they wander too far from forested areas (Mattson et al. 1992). Grizzly claws have evolved primarily for digging; black bears have evolved more curved claws that allow them to climb trees (Herrero 1972, 1978, Stirling and Derocher 1990). Likewise, thick vegetation provides concealment for bears (Pelton 2000) and can serve as an auditory warning system of approaching danger (Costello et al. 2001).

Black bear populations can suffer increased mortality because of movements associated with seasonality of food resources (Garshelis and Pelton 1981, Rogers 1987, Beck 1991, McDonald et al. 1994, Samson and Huot 1998), disjunct habitat patches (Rogers 1987, Maehr et al. 1988, Elowe and Dodge 1989, Stratman et al. 2001b), and dispersal of subadult males (Beecham 1983, Bunnell and Tait 1985, Beck 1991, Schwartz and Franzmann 1992, Wertz et al. 2001). Therefore, protective travel corridors are required to provide safe movement into and out of habitats due to mortality associated with vehicular collisions and hunting pressure during such movements (Beecham 1983, McDonald et al. 1994, Wooding and Hardisky 1994, Stratman et al. 2001b, Wertz et al. 2001). Habitats that provide effective travel corridors typically consist of dense, unmanaged forests located along creek and river drainages, ridgetops, or gaps (Mollohan et al. 1989, Pelton 2000, Wertz et al. 2001).

Although the above outlined factors are the basic components driving habitat selection, interactions among these factors vary across different scales, likely resulting in alternate use patterns depending upon the fractal nature of the landscape and the perception of these factors at different scales (O’Neill et al. 1988, Ritchie 1998). The fractal nature of many landscapes results from varying sizes and distributions of resource patches. This fractal nature is at the heart of habitat selection, as the scale at which an individual perceives the environment influences how habitat factors are perceived and the abundance of resources it detects (O’Neill et al. 1988, With

1994, Ritchie 1998). For example, a bear may perceive a given fractal habitat as having only a few large patches or may perceive this same habitat as having many small patches nested within 1 to several larger patches (Wiens 1989, Ritchie 1998). Therefore, an understanding of how bears are selecting patches (i.e., selection of food patches through complete random utilization or complete discrimination) should result in more efficient habitat models and is a necessary step for delineating critical habitats.

Habitat selection is typically defined at four different scales: 1) selection of the species geographic range, 2) selection of an individuals home-range within the landscape, 3) selection of different habitat patches within the home-range (termed stand selection), and 4) selection of site specific areas (i.e., feeding and resting sites) (Johnson 1980, Lofroth 1993). These different levels reflect the hierarchical nature of resource selection (Johnson 1980, Aebischer et al. 1993, Anderson and Gutzwiller 1996) and reinforce the idea that the context of spatial scale is only relevant after examining habitat use across scales (O'Neill et al. 1988, Kotliar and Wiens 1990, Lord and Norton 1990, Apps et al. 2001). Nonetheless, habitat selection at the first scale is typically ignored.

The importance of different scales varies among species. Landscape level features can be the overriding factor in determining habitat suitability of some animals (e.g., spotted owl [*Strix occidentalis*]; Hansen et al. 1993) while smaller-scale factors are more important for others (e.g., bison [*Bison bison*], Fortin et al. 2003; elk, Jones and Hudson 2002). However, the more likely result is selection at multiple scales, resulting in a hierarchy that explains selection at progressively higher or lower levels (Pedlar et al. 1997, Jones and Hudson 2002, Weir and Harestad 2003). Such a hierarchy should allow for the construction of models that relate site-specific parameters to stand and/or landscape components resulting in more effective and applicable models (Mysterud et al. 1999, Weir and Harestad 2003).

To my knowledge, only Clark et al. (1993) and Lyons et al. (2003) have assessed habitat use of American black bears across multiple scales (they assessed second and third order selection), though Carr et al. (2002) determined habitat use across 2 scales for Asiatic black bears and Gautestad et al. (1998) developed models that used scale-free habitat use to assess home-range selection in black bears. Nonetheless, numerous studies have assessed habitat selection at specific scales (e.g., landscape [Jones et al. 1998, Samson and Huot 1998, Beckmann and Berger 2003b]; stand [Hellgren et al. 1991, Wooding and Hardisky 1994, Stratman et al. 2001a, Fecske et al. 2002]; site-specific [Mollohan et al. 1989, Bull et al. 2001, Cunningham et al. 2003]). Numerous factors have been identified as potential components involved in habitat selection. The following paragraphs provide an explanation of these variables.

Geophysical and environmental characteristics.—Factors in this category include slope, terrain ruggedness, aspect, soil type, geologic unit, elevation, climatic values, and actual evapotranspiration (AET). Slope has been shown to be a significant factor in habitat selection for bears, as steeper slopes provide greater protection for resting, foraging, and denning locations (Beecham 1980, LeCount 1983b, Mollohan et al. 1989, Zeigenfuss 2001). Related to slope are indices of terrain ruggedness (e.g., Land Surface Ruggedness Index, Beasom 1983; landform index, McNab 1993). These indices provide an estimate of topographical relief in an area. Rugged areas are preferential locations for denning (Mack 1990) and provide superb escape cover for bears (Mollohan et al. 1989). Aspect can be an important factor in determining den sites (presumably for increased insulation and reduction of spring flooding; Beecham et al. 1983, Rogers 1987) but directionality differs by locality (i.e., western, Washington [Lindzey and

Meslow 1976a]; southern, California [Novick et al. 1981]; northeastern, Arizona [LeCount 1983a]). In RMNP, bears typically select north and east facing slopes (Baldwin 2008). Aspect also affects vegetative productivity and composition (e.g., Beecham and Rohlman 1994, Sternberg and Shoshany 2001), thus providing a potential influence on habitat selection. Soils greatly influence the productivity of an area (Rogers 1987, Rogers and Allen 1987, Noyce and Coy 1990). Knowledge of present soils should serve as an index of productivity across the landscape. Underlying geologic units are greatly responsible for soil types present (e.g., Burke 2002), and could also be an important factor in determining bear use of an area.

Food abundance and maturation can be heavily influenced by the elevation in an area (i.e., effect of stacked life-zones; Brown and Lomolino 1998). In locations such as RMNP, bears are known to follow elevational gradients as seasons progress to maximize food consumption (Beck 1991). Additionally, substantial climatic differences are observed across different elevational gradients (i.e., differences in temperatures and precipitation amounts). These climatic differences can lead to differences in vegetative productivity. This difference in productivity is an important factor to consider, as the influence of climate on habitat can have long term effects on population size (Beecham 1983, Johnson et al. 2002, Bender and Weisenberger 2005). AET is a tool often used to assess vegetative productivity across different watersheds and landscapes (Rosenzweig 1968, Whittaker 1975, Badgley and Fox 2000). Measurements of AET are related to moisture loss from evaporation and transpiration (thus measuring the simultaneous availability of water and solar energy; Rosenzweig 1968) and are determined under actual conditions of moisture supply (Badgley and Fox 2000). These values are used as surrogates of vegetative productivity and have had extensive utility in predicting species distributions (Whittaker 1975, Badgley and Fox 2000). AET may be an effective large-scale tool in assessing productivity for bears in RMNP.

Forest characteristics.—General covertype is the most frequently assessed variable in habitat studies (e.g., Lindzey and Meslow 1977b, Hellgren et al. 1991, Costello et al. 2001) due to the strong relationship between cover/stand type and bear use. Vertical cover represents a measure of visual obstruction and vegetative density, and has been implicated as a principal factor influencing habitat selection of black bears in Arizona (Mollohan et al. 1989).

Canopy cover has several effects on habitat quality including visual obstruction, precipitation and radiation interception, a strong negative relationship to forage production, an insulative influence on temperature, humidity, and wind speed, and can override all other variables in determining understory development and potentially composition (Hoefs and Shay 1981, Parker 1995, Bull et al. 2001). All these factors, either singularly or cumulative, could influence habitat selection (Rogers et al. 1988). Stand height has been assessed in several studies (i.e., Hayes and Pelton 1994, Martorello and Pelton 2003) and is a reflection of age and structure of a stand.

An alternative assessment of vertical structure is represented through total basal area (BA) but only reflects cover associated with trees. Relating size classes of trees to basal area measurements also provides insight into the seral stage of forests. Additionally, BA of large trees is often recorded, as large trees can provide suitable denning and refuge sites (e.g., Rogers and Allen 1987, Mitchell et al. 2002, Mitchell and Powell 2003). In contrast to vertical cover, basal area measurements are often included in standard GIS maps, thus providing a variable that can easily be assessed across various scales.

Several studies have noted the importance of logs and snags for denning (Lindzey and Meslow 1976a, Davis 1996), resting (R. Baldwin, personal observation), and foraging locations (Rogers et al. 1988, Noyce et al. 1997, Bull et al. 2001, Mitchell and Powell 2003). These could potentially be very important components for bears in RMNP, as insects comprise a large part of bear diets in RMNP (Zeigenfuss 2001). Burn locations often contain a large number of snags and logs. Additionally, they typically contain early successional species which are important food sources for bears (Rogers et al. 1988, Mattson 1990, Schwartz and Franzmann 1991, Samson and Huot 1998). Many food items are often associated with wetlands, streams, and lakes (Rogers et al. 1988). Additionally, wetlands can aid in thermoregulation during warm days (Rogers et al. 1988). Therefore, distances and densities of these factors could be important factors in habitat selection.

Size and density of habitat patches were implicated as important characteristics defining black bear habitats (Jonkel and Cowan 1971, Rogers et al. 1988, Mollohan et al. 1989, Mitchell and Powell 2003). Likewise, several investigators have noted the importance of habitat juxtaposition and forest diversity to black bears (Lindzey and Meslow 1977b, Clark et al. 1993, Jones et al. 1998, Koehler and Pierce 2003). Therefore, patch size, patch density, and contagion (an index of habitat heterogeneity) could be related to bear locations to determine their influence on habitat selection.

Food.—The importance of food in habitat selection has been discussed in detail above. Nonetheless, assessments of food biomass should provide good indications of preferred habitats (e.g., Rogers 1976, Noyce and Coy 1990, Costello and Sage 1994). However, biomass only reflects food available; it does not define preferred foods. Food selection by bears should be positively related to body condition. Since body condition is related to various reproductive parameters and ultimately survival, bears should be selecting those habitats which provide the greatest abundance of preferred foods. Therefore, understanding how and why bears select foods should yield insight into habitat selection. To help relate food use to habitat selection, Kansas and Raine (1990) introduced a food importance value which Clark et al. (1994) further developed into a food value index (FVI) that incorporated average percent cover, mean food production, and average frequency of occurrence in scats. These values were then summed to determine FVI's for each forest type. Similar techniques could be useful to assess the relationship between what is available and what is consumed.

Nutritional components are known to influence productivity in bears and may serve as good indicators of habitat quality, as well (Elowe and Dodge 1989, Kasbohm et al. 1995, Noyce et al. 1997). Relating digestive and metabolic efficiencies of different foods to associated body condition indices should yield insight into critical habitats for bears, ultimately discerning those factors exerting the greatest influence on survival and reproduction. These values can be assessed for an entire site, but can also be combined with food value indices to determine nutritional quality selected.

Human influence.—Presence of humans can greatly impact bear populations and subsequently, habitat selection. Heavy human-use areas can result in avoidance of associated areas (McCutchen 1990, van Manen 1994, van Manen and Pelton 1997, Chi and Gilbert 1999) or can serve as attractants due to abundant energy-rich food sources (Barnes 1967, Herrero 1983, Beckmann and Berger 2003b). Remote buildings and backcountry campsites elicit similar responses (Jonkel and Cowan 1971, Keay and van Wagtendonk 1983). Therefore, these factors must be considered when determining critical bear habitats.

Several investigators have assessed the influence of roads and trails on bear occurrence (i.e., Garner 1986, Beringer et al. 1990, Hellgren et al. 1991, Zeigenfuss 2001). This influence appears to be affected by the level of use. Heavily used roads and trails typically elicit avoidance responses (Garner 1986, Beringer et al. 1990, van Manen 1994, Fecske et al. 2002). However, if traffic is minimal, they may be selected for, as bears will use roads and trails as foraging locations (associated with increased early successional species) and travel corridors (Jonkel and Cowan 1971, Manville 1983, Hellgren et al. 1991, Bull et al. 2001). Therefore, the level of use of roads and trails should be included in analyses to better understand the suitability of associated habitats.

Habitat modeling

Determination of habitat use is often accomplished through modeling. Many different forms exist, but the Habitat Suitability Index (HSI) and nutritional carrying capacity (NCC) models are 2 of the better known techniques. Habitat Suitability Index models are designed to reflect critical habitats in measurable units through an index of carrying capacity that is proportional to that of the actual habitat (Anderson and Gutzwiller 1996). Typically, scores of models are based on a scale of 0.0–1.0 (0.0 reflecting unsuitable habitat, 1.0 optimal habitat) that reflect the percentage of the maximum habitat capability (Bender et al. 1996). Construction of HSI's involves establishing species habitat requirements, developing the model, and determining HSI's for available habitat (Anderson and Gutzwiller 1996). Models are typically constructed from literature reviews or researcher judgment and often include several major components including food, cover, habitat interspersion, indicators of human disturbance, and special requirements for reproduction (i.e., den sites for bears; Rogers and Allen 1987, Zimmerman

1992). Once constructed, data can be collected to determine the capability of a habitat to support "x" number of individuals.

Habitat Suitability Indices generally yield linear models that are simple to understand. Additionally, these models are applicable across large spatial scales and are widely included into management plans (Roloff and Kernohan 1999). However, this method is hindered by several problems including limited field evaluation, an oversimplified view of habitat interactions, a lack of variance estimates, and the inability to relate index scores to actual productivity parameters (Anderson and Gutzwiller 1996, Bender et al. 1996, Roloff and Kernohan 1999). Nonetheless, HSI's have been published for black bears in the upper great lakes region (Rogers and Allen 1987) and in the southern Appalachian region (Zimmerman 1992, Powell et al. 1997, Mitchell et al. 2002, Mitchell and Powell 2003). Rogers and Allen (1987) never tested their model, but acknowledged the need to do so. Hirsch and Haufler (1993) did test Rogers and Allen's (1987) model and determined that habitat quality for Drummond Island, Michigan, was low (0.27). However, this did not reflect known productivity parameters, suggesting that the model required significant revision. Models constructed in the southern Appalachian region were tested and yielded a strong relationship between the HSI and actual habitat selection (Zimmerman 1992, Mitchell et al. 2002). However, Garshelis (2000) noted the need to also associate demographic vigor (i.e., reproduction, juvenile growth rate, etc.; Hanks 1978) to such models. Unfortunately, such relationships are often beyond the scope of HSI's (though inclusion of a nutritional/food component may allow such a relationship). Therefore, even if accurate HSI models can be constructed and validated, they typically lack the ability to directly relate to fitness/productivity parameters.

Nutritional carrying capacity models allow direct estimation of carrying capacity, therefore determining a specific number of individuals a habitat can support (Robbins 1973, Hobbs and Swift 1985). Measures of NCC usually relate to quantity and quality of forage or their associated interaction. For example, McCall et al. (1997) measured range supplies of dry matter, digestible energy, digestible nitrogen, dry matter × digestible energy, and dry matter × digestible nitrogen to determine carrying capacity of rangeland in Texas for white-tailed deer. Additionally, some investigations have incorporated the nutritional condition of the animal, along with the prior outlined variables, to develop a more accurate estimate (e.g., McCall et al. 1997).

A major advantage of NCC models over HSI's is that they allow the user to specifically predict habitat capability, thus allowing direct comparisons to productivity parameters. However, these models are typically complex and rely on the assumption that forage is equally available throughout the habitat, thus making extrapolation difficult across larger scales (McCall et al. 1997). They also fail to account for additional landscape effects that may influence habitat suitability (i.e., road density, escape cover, etc.). Therefore, NCC models are generally used only for relative assessments of carrying capacity (McCall et al. 1997).

Although these 2 methods have limitations, a combination of their attributes may have applicability. Animal production is directly related to net energy gains (Cook et al. 2002). Therefore, an understanding of the inherent ability of habitat patches to produce net energy gains should be useful in determining critical habitats. However, all aspects of habitat selection (i.e., food, water, denning locations, escape cover, and movement corridors) must be considered in determining the realized value of habitat patches. For example, road densities can have a negative influence on bears (Garner 1986, Beringer et al. 1990). Therefore, buffers must be placed around roads to account for the reduction in inherent values of associated habitats. Nonetheless, the relationship of body condition to habitats selected should yield models that are applicable at larger spatial scales, are linked with management practices, incorporate forage quality and quantity, and allow for the prediction of fitness/productivity parameters.

Likewise, such assessments should lead to a better understanding of how bears are selecting resources spatially. Three basic theories exist regarding habitat selection: 1) complete discrimination (CD; Pulliam 1996), 2) ideal despotic distribution (IDD; Fretwell 1972), and 3) complete random utilization (CRU; Pulliam 1996). The underlying theory behind CD is that each individual in a population will seek to use that habitat which provides the greatest net energy gain. They will only utilize lesser quality habitats if populations become so saturated that it is more energetically beneficial to utilize such habitats (i.e., the value of the preferred habitat is deteriorated to the point that the second most preferred habitat is selected, etc). Such a situation implies that fitness measures are equal across the entire range (Beckmann and Berger 2003b). Ideal despotic distribution implies that dominant individuals preferentially select “prime” habitats and exclude subordinates. Such exclusion leads to unequal fitness measurements across the landscape (Messier et al. 1990). Complete random utilization infers no prior knowledge of surrounding habitats. Individuals select habitats simply by chance.

An IDD model has been proposed by Beckmann and Berger (2003b) for black bears in the Lake Tahoe region, California. However, this population existed at an urban/wildland interface where abundant food sources existed in well defined patches (i.e., garbage). In this situation, large males excluded females from foraging sites. Similar results have been observed for garbage dumps (Rogers 1987), berry patches (Jonkel and Cowan 1971, Rogers 1987), and oak stands (Garshelis and Pelton 1981). Nonetheless, this behavior is typically only seen in areas where such well-defined patches exist. No apparent patches have been found in RMNP, suggesting that the local population will not conform to IDD.

Complete discrimination models have several underlying assumptions: 1) foragers act to maximize foraging efficiency, 2) they have perfect knowledge of resources (this may be an inappropriate assumption if animals are not always feeding. In such a situation, exploratory movements allow individuals to locate higher quality patches without having perfect knowledge of the area.), 3) they have equal competitive abilities, and 4) individual resource capture decreases with increased competition (Kennedy and Gray 1993). Unfortunately, one or more of these assumptions are often not met (i.e., individuals over-use poor sites and under-use prime sites; Kennedy and Gray 1993). Many factors could account for this including population densities, presence of anthropogenic factors (i.e., campgrounds and roads), and age and size structures of the population resulting in competitive advantages for some (i.e., smaller females better suited for climbing cherry trees than larger males; Garner 1986). Nonetheless, CD should serve as a good starting point for assessing spatial patterns in habitat use. Once landscape effects are determined, they can be incorporated into the model to increase accuracy.

As stated earlier, CRU models infer no prior knowledge or selection preference within the landscape. However, this does not appear to apply to bears, as many long-range movements to food patches have been observed (Jonkel and Cowan 1971, Rogers 1987, Elowe and Dodge 1989, Schwartz and Franzmann 1991). Therefore, it is likely that habitat selection for bears in RMNP falls somewhere between CD and CRU. Measures of this distribution should help in determining critical habitats in RMNP.

LITERATURE CITED

Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74:1313–1325.

Akenson, J. J., M. G. Henjum, T. L. Wertz, and T. J. Craddock. 2001. Use of dogs and mark-recapture techniques to estimate American black bear density in northeastern Oregon. Ursus 12:203–210.

Alt, G. L. 1981. Reproductive biology of black bears of Northeastern Pennsylvania. Transactions of the Northeast Fish and Wildlife Conference 38:88–89.

Alt, G. L. 1984. Black bear cub mortality due to flooding of natal dens. Journal of Wildlife Management 48:1432–1434.

Alt, G. L. 1989. Reproductive biology of female black bears and early growth and development of cubs in northeastern Pennsylvania. Dissertation, West Virginia University, Morgantown, West Virginia, USA.

Alt, G. L., G. J. Matula, Jr., F. W. Alt, and J. S. Lindzey. 1980. Dynamics of Home range and movements of adult black bears in northeastern Pennsylvania. International Conference on Bear Research and Management 4:131–136.

Amstrup, S. C., and J. Beecham. 1976. Activity patterns of radio-collared black bears in Idaho. Journal of Wildlife Management 40:340–348.

Anderson, D. R. 2001. The need to get the basics right in wildlife field studies. Wildlife Society Bulletin 29:1294–1297.

Anderson, D. R. 2003. Response to Engeman: index values rarely constitute reliable information. Wildlife Society Bulletin 31:288–291.

Anderson, S. H., and K. J. Gutzwiller. 1996. Habitat evaluation methods. Pages 592–606 *in* T. A. Bookhout, editor. Research and management techniques for wildlife and habitats. Fifth edition. The Wildlife Society, Bethesda, Maryland, USA.

Apps, C. D., B. N. McLellan, T. A. Kinley, and J. P. Flaa. 2001. Scale-dependent habitat selection by mountain caribou, Columbia Mountains, British Columbia. Journal of Wildlife Management 65:65–77.

Arnould, J. P. Y., and M. A. Ramsay. 1994. Milk production and milk consumption in polar bears during the ice-free period in western Hudson Bay. Canadian Journal of Zoology 72:1365–1370.

Aschoff, J. 1964. Survival value of diurnal rhythms. Symposia of the Zoological Society of London 13:79–98.

Atkinson, S. N., R. A. Nelson, and M. A. Ramsay. 1996. Changes in the body composition of fasting polar bears (*Ursus maritimus*): the effect of relative fatness on protein conservation. Physiological Zoology 69:304–306.

Atkinson, S. N., and M. A. Ramsay. 1995. Effects of prolonged fasting on the body composition and reproductive success of adult female polar bears (*Ursus maritimus*). Functional Ecology 9:559–567.

Ayres, L. A., L. S. Chow, and D. M. Graber. 1986. Black bear activity patterns and human induced modifications in Sequoia National Park. International Conference on Bear Research and Management 6:151–154.

Badgley, C., and D. L. Fox. 2000. Ecological biogeography of North American mammals: species density and ecological structure in relation to environmental gradients. Journal of Biogeography 27:1437–1467.

Barnes, V. G., Jr. 1967. Activities of black bears in Yellowstone National Park. Thesis, Colorado State University, Fort Collins, Colorado, USA.

Barnes, V. G., Jr., and O. E. Bray. 1966. Black bears use drainage culverts for winter dens. Journal of Mammalogy 47:712–713.

Beasom, S. L. 1983. A technique for assessing land surface ruggedness. Journal of Wildlife Management 47:1163–1165.

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

Beck, T. D. I. 1995. Development of black bear inventory techniques. Colorado Division of Wildlife Federal Aid Progress Report W-153-R-8, WP5A, J2. Fort Collins, Colorado, USA.

Beck, T. D. I. 1997. Development of black bear inventory techniques. Colorado Division of Wildlife Federal Aid Progress Report W-153-R-10, WP5A, J2. Fort Collins, Colorado, USA.

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

Beecham, J. J. 1980. Some population characteristics of two black bear populations in Idaho. International Conference on Bear Research and Management 4:201–204.

Beecham, J. J. 1983. Population characteristics of black bears in west central Idaho. Journal of Wildlife Management 47:405–412.

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.

Beecham, J. J., and J. Rohlman. 1994. A shadow in the forest: Idaho's black bear. Idaho Department of Fish and Game, Boise, and University of Idaho Press, Moscow, Idaho, USA.

Beeman, L. E., and M. R. Pelton. 1980. Seasonal foods and feeding ecology of black bears in the Smoky Mountains. International Conference on Bear Research and Management 4:141–147.

Bender, L. C., and J. G. Cook. 2005. Nutritional condition of elk in Rocky Mountain National Park. Western North American Naturalist 65:329–334.

Bender, L. C., and B. J. Keller. 2005. Behavioral implications of bighorn sheep (*Ovis canadensis canadensis*) use of the Sheep Lakes mineral site, Rocky Mountain National Park, Colorado. Final Report, U.S. National Park Service—Rocky Mountain National Park.

Bender, L. C., L. A. Lomas, and T. Kamienski. 2007. Habitat effects on condition of mule deer in arid mixed woodland-grassland. Rangeland Ecology and Management 60:277–284.

Bender, L. C., G. J. Roloff, and J. B. Haufler. 1996. Evaluating confidence intervals for habitat suitability models. Wildlife Society Bulletin 24:347–352.

Bender, L. C., and M. E. Weisenberger. 2005. Precipitation, density, and population dynamics of desert bighorn sheep on San Andres National Wildlife Refuge, New Mexico. Wildlife Society Bulletin 33:956–964.

Bennett, L. J., P. F. English, and R. L .Watts. 1943. The food habits of the black bear in Pennsylvania. Journal of Mammalogy 24:25–31.

Berg, R. T., and R. M. Butterfield. 1976. New concepts of cattle growth. Sydney University Press, Sydney, Australia.

Beringer, J. J., S. G. Seibert, and M. R. Pelton. 1990. Incidence of road crossing by black bears on Pisgah National Forest, North Carolina. International Conference on Bear Research and Management 8:85–92.

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

Bertram, M. R., and M. T. Vivion. 2002. Black bear monitoring in eastern interior Alaska. Ursus 13:69–77.

Bjarvall, A., and F. Sandegren. 1987. Early experiences with the first radio-marked brown bears in Sweden. International Conference on Bear Research and Management 7:9–12.

Boersen, M. R., J. D. Clark, and T. L. King. 2003. Estimating black bear population density and genetic diversity at Tensas River, Louisiana using microsatellite DNA markers. Wildlife Society Bulletin 31:197–207.

Brandenburg, D. M. 1996. Effects of roads on behavior and survival of black bears in coastal North Carolina. Thesis, University of Tennessee, Knoxville, Tennessee, USA.

Brody, A. J., and M. R. Pelton. 1988. Seasonal changes in digestion in black bears. Canadian Journal of Zoology 66:1482–1484.

Brown, J. H., and M. V. Lomolino. 1998. Biogeography. Second edition, Sinauer Associates, Incorporated, Sunderland, Massachusetts, USA.

Brown, J. L. 1964. The evolution of diversity in avian territorial systems. Wilson Bulletin 76:160–169.

Bull, E. L., T. W. Heater, and T. L. Wertz. 2001. Black bear habitat use in northeastern Oregon. Western Black Bear Workshop 7:82–91.

Bunnell, F. L., and T. Hamilton. 1983. Forage digestibility and fitness in grizzly bears. International Conference on Bear Research and Management 5:179–185.

Bunnell, F. L., and D. E. N. Tait. 1980. Bears in models and reality—implications to management. International Conference on Bear Research and Management 4:15–23.

Bunnell, F. L., and D. E. N. Tait. 1981. Population dynamics of bears—implications. Pages 75–98 *in* C. W. Fowler and T. D. Smith, editors. Dynamics of large mammal populations. John Wiley and Sons, Inc., New York, USA.

Bunnell, F. L., and D. E. N. Tait. 1985. Mortality rates of North American bears. Arctic 38:316–323.

Bunting, S. 1996. The use and role of fire in natural areas. Pages 277–301 *in* R. G. Wright, editor. National parks and protected areas: their role in environmental protection. Blackwell Scientific, Cambridge, Massachusetts, USA.

Burke, A. 2002. Properties of soil pockets on arid Nama Karoo inselbergs-the effect of geology and derived landforms. Journal of Arid Environments 50:219–234.

Burst, T. L., and M. R. Pelton. 1983. Black bear mark trees in the Smoky Mountains. International Conference on Bear Research and Management 5:45–53.

Calder, W. A., III. 1984. Size, function, and life history. Harvard University Press, Cambridge, Massachusetts, USA.

Carlock, D. M. 1986. Preliminary results of three years of bait-station surveys for black bears in north Georgia. Proceedings of the Eastern Workshop on Black Bear Research and Management 8:118–124.

Carpenter, F. L., and R. E. MacMillen. 1976. Threshold model of feeding territoriality and test with a Hawaiian honeycreeper. Science 194:639–642.

Carpenter, M. 1973. The black bear in Virginia. Virginia Commission of Game and Inland Fisheries, Richmond, Virginia, USA.

Carr, M. M., J. Yoshizaki, F. T. van Manen, M. R. Pelton, O. C. Huygens, H. Hayashi, and M. Maekawa. 2002. A multi-scale assessment of habitat use by Asiatic black bears in central Japan. Ursus 13:1–9.

Cattet, M. 1990. Predicting nutritional condition in black bears and polar bears on the basis of morphological and physiological measurements. Canadian Journal of Zoology 68:32–39.

Cattet, M. R. L., S. N. Atkinson, S. C. Polischuk, and M. A. Ramsay. 1997. Predicting body mass in polar bears: is morphometry useful? Journal of Wildlife Management 61:1083–1090.

Cattet, M. R. L., N. A. Caulkett, M. E. Obbard, and G. B. Stenhouse. 2002. A body-condition index for ursids. Canadian Journal of Zoology 80:1156–1161.

Caughley, G. 1974. Interpretation of age ratios. Journal of Wildlife Management 38:557–562.

Chan-McLeod, A. C. A., R. G. White, and D. E. Russell. 1995. Body mass and composition indices for female barren-ground caribou. Journal of Wildlife Management 59:278–291.

Chi, D. K., and B. K. Gilbert. 1999. Habitat security for Alaskan black bears at key foraging sites: are there thresholds for human disturbance. Ursus 11:225–238.

Clapp, D. L. 1990. Availability and consumption of foods and importance of habitats used by black bears in Arkansas. Thesis, University of Arkansas, Fayetteville, Arkansas, USA.

Clark, J. D. 2004. Oak-black bear relationships in southeastern uplands. Pages 116–119 *in* M. A. Spetich, editor. Upland oak ecology symposium: history, current conditions, and sustainability. General Technical Report SRS-73. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, North Carolina, USA.

Clark, J. D., J. E. Dunn, and K. G. Smith. 1993. A multivariate model of female black bear habitat use for a Geographic Information System. Journal of Wildlife Management 57:519–526.

Clark, J. D., D. L. Clapp, K. G. Smith, and B. Ederington. 1994. Black bear habitat use in relation to food availability in the interior highlands of Arkansas. International Conference on Bear Research and Management 9:309–318.

Clark, J. D., and K. G. Smith. 1994. A demographic comparison of two black bear populations in the interior highlands of Arkansas. Wildlife Society Bulletin 22:593–603.

Clevenger, A. P., and F. J. Purroy. 1996. Sign surveys for estimating trend of a remnant brown bear *Ursus arctos* population in northern Spain. Wildlife Biology 2:275–281.

Cook, J. G., R. C. Cook, L. C. Bender, B. Hall, and L. L. Irwin. 2002. Nutritional influences on northwestern elk herds: wild elk capture and nutritional condition assessment. Progress Report, National Council for Air and Stream Improvement, La Grande, Oregon, USA.

Cook, R. C., J. G. Cook, D. L. Murray, P. Zager, B. K. Johnson, and M. W. Gratson. 2001. Development of predictive models of nutritional condition for Rocky Mountain elk. Journal of Wildlife Management 65:973–987.

Costello, C. M. 1992. Black bear habitat ecology in the central Adirondacks as related to food abundance and forest management. Thesis, State University of New York, Syracuse, New York, USA.

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, New Mexico, USA.

Costello, C. M., D. E. Jones, R. M. Inman, K. H. Inman, B. C. Thompson, and H. B. Quigley. 2003. Relationship of variable mast production to American black bear reproductive parameters in New Mexico. Ursus 14:1–16.

Costello, C. M., and R. W. Sage, Jr. 1994. Predicting black bear habitat selection from food abundance under 3 forest management systems. International Conference on Bear Research and Management 9:375–387.

Craighead, J. J., J. R. Varney, F. C. Craighead, Jr., and J. S. Sumner. 1976. Telemetry experiments with a hibernating black bear. International Conference on Bear Research and Management 3:357–371.

Cunningham, S. C., W. B. Ballard, L. M. Monroe, M. J. Rabe, and K. D. Bristow. 2003. Black bear habitat use in burned and unburned areas, central Arizona. Wildlife Society Bulletin 31:786–792.

Davis, H. 1996. Characteristics and selection of winter dens by black bears in coastal British Columbia. Thesis, Simon Fraser University, Burnaby, British Columbia, Canada.

Davis, R. W. 2005. A GIS-based habitat model for predicting elk nutritional condition in the Pacific Northwest. Dissertation, University of Illinois, Urbana, Illinois, USA.

DeBruyn, T. D. 1992. Home range size, food habits and habitat use of female black bears in the central upper peninsula of Michigan. Thesis, Northern Michigan University, Marquette, Michigan, USA.

DelGiudice, G. D., L. L. Rogers, A. W. Allen, and U. S. Seal. 1991. Weights and hematology of wild black bears during hibernation. Journal of Wildlife Diseases 27:637–642.

Doan-Crider, D. L., and E. C. Hellgren. 1996. Population characteristics and winter ecology of black bears in Coahuila, Mexico. Journal of Wildlife Management 60:398–407.

Eagle, T. C., and M. R. Pelton. 1983. Seasonal nutrition of black bears in the Great Smoky Mountains National Park. International Conference on Bear Research and Management 5:94–101.

Eason, T. H., B. H. Smith, and M. R. Pelton. 1996. Researcher variation in collection of morphometrics on black bears. Wildlife Society Bulletin 24:485–489.

Eberhardt, L. L. 1990. Survival rates required to sustain bear populations. Journal of Wildlife Management 54:587–590.

Eiler, J. H., W. G. Wathen, and M. R. Pelton. 1989. Reproduction in black bears in the southern Appalachian Mountains. Journal of Wildlife Management 53:353–360.

Elowe, K. D. 1984. Home range, movements, and habitat preferences of black bear (*Ursus americanus*) in western Massachusetts. Thesis, University of Massachusetts, Amherst, Massachusetts, USA.

Elowe, K. D., and W. E. Dodge. 1989. Factors affecting black bear reproductive success and cub survival. Journal of Wildlife Management 53:962–968.

Engeman, R. M. 2003. More on the need to get the basics right: population indices. Wildlife Society Bulletin 31:286–287.

Erickson, A. W., J. Nellor, and G. A Petrides. 1964. The black bear in Michigan. Michigan State University Agricultural Experiment Station Research Bulletin Number 4.

Erickson, A. W., and W. G. Youatt. 1961. Seasonal variations in the hematology and physiology of black bears. Journal of Mammalogy 41:198–203.

Farley, S. D., and C. T. Robbins. 1994. Development of two methods to estimate body composition of bears. Canadian Journal of Zoology 72:220–226.

Fecske, D. M., R. E. Barry, F. L. Precht, H. B. Quigley, S. L. Bittner, and T. Webster. 2002. Habitat use by female black bears in western Maryland. Southeastern Naturalist 1:77–92.

Folk, G. E., Jr. 1967. Physiological observations on subarctic bears under winter den conditions. Pages 78–85 *in* K. Fisher and F. South, editors. Mammalian hibernation III. American Elsevier Publishing Company, Inc., New York, USA.

Folk, G. E., Jr., M. A. Folk, and J. J. Minor. 1972. Physiological condition of three species of bears in winter dens. International Conference on Bear Research and Management 2:107–124.

Folk, G. E., Jr., J. M. Hunt, and M. A. Folk. 1976. Further evidence for hibernation of bears. International Conference on Bear Research and Management 3:43–47.

Fortin, D., J. M. Fryxell, L. O'Brodovich, and D. Frandsen. 2003. Foraging ecology of bison at the landscape and plant community levels: the applicability of energy maximization principles. Oecologia 134:219–227.

Fowler, C. W. 1981. Density dependence as related to life history strategy. Ecology 62:602–610.

Franzmann, A. W. 1985. Assessment of nutritional status. Pages 239–260 *in* R. J. Hudson and R. G. White, editors. Bioenergetics of wild herbivores. CRC Press, Boca Raton, Florida, USA.

Franzmann, A. W., and C. C. Schwartz. 1986. Black bear predation on moose calves in highly productive versus marginal moose habitats on the Kenai Peninsula, Alaska. Alces 22:139–154.

Free, S. L., and E. McCaffrey. 1972. Reproductive synchrony in the female black bear. International Conference on Bear Research and Management 2:26–31.

Freedman, A. H., K. M. Portier, and M. E. Sunquist. 2003. Life history analysis for black bears (*Ursus americanus*) in a changing demographic landscape. Ecological Modelling 167:47–64.

Fretwell, S. D. 1972. Populations in a seasonal environment. Monographs in population biology 5. Princeton University Press, Princeton, New Jersey, USA.

Fuller, D. P. 1993. Black bear population dynamics in western Massachusetts. Thesis, University of Massachusetts, Amherst, Massachusetts, USA.

Gaillard, J.-M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology and Evolution 13:58–63.

Gaillard, J.-M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toïgo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31:367–393.

Gales, R., D. Renouf, and G. A. J. Worthy. 1994. Use of bioelectrical impedance analysis to assess body composition of seals. Marine Mammal Science 10:1–12.

Garner, N. P. 1986. Seasonal movements, habitat selection, and food habits of black bears (*Ursus americanus*) in Shenandoah National Park, Virginia. Thesis, Virginia Polytechnic Institute and State University, Blacksburg, Virginia, USA.

Garshelis, D. L. 1990. Monitoring effects of harvest on black bear populations in North America: a review and evaluation of techniques. Proceedings of the Eastern Workshop on Black Bear Research and Management 10:120–144.

Garshelis, D. L. 2000. Delusions in habitat evaluation: measuring use, selection, and importance. Pages 111–164 *in* L. Boitani and T. K. Fuller, editors. Research techniques in animal ecology. Columbia University Press, New York, New York, USA.

Garshelis, D. L. 2002. Misconceptions, ironies, and uncertainties regarding trends in bear populations. Ursus 13:321–334.

Garshelis, D. L., and M. R. Pelton. 1979. Use of telemetric motion sensors for monitoring activity of black bears. Proceedings of the Eastern Workshop on Black Bear Management and Research 4:220–225.

Garshelis, D. L., and M. R. Pelton. 1980. Activity of black bears in the Great Smoky Mountains National Park. Journal of Mammalogy 61:8–19.

Garshelis, D. L., and M. R. Pelton. 1981. Movements of black bears in the Great Smoky Mountains National Park. Journal of Wildlife Management 45:912–925.

Garshelis, D. L., H. B. Quigley, C. R. Vilarrubia, and M. R. Pelton. 1982. Assessment of telemetric motion sensors for study of activity. Canadian Journal of Zoology 60:1800–1805.

Garshelis, D. L., H. B. Quigley, C. R. Vilarrubia, and M. R. Pelton. 1983. Diel movements of black bears in the southern Appalachians. International Conference on Bear Research and Management 5:11–19.

Garshelis, D. L., and L. G. Visser. 1997. Enumerating megapopulations of wild bears with an ingested biomarker. Journal of Wildlife Management 61:466–480.

Gau, R. J., and R. Case. 1999. Evaluating nutritional condition of grizzly bears via select blood parameters. Journal of Wildlife Management 63:286–291.

Gau, R. J., and R. Case. 2002. Evaluating nutritional condition of grizzly bears via ^{15}N signatures and insulin-like growth factor-1. Ursus 13:285–291.

Gautestad, A. O., I. Mysterud, and M. R. Pelton. 1998. Complex movement and scale-free habitat use: testing the multi-scaled home-range model on black bear telemetry data. Ursus 10:219–234.

Gerhart, K. L., R. G. White, R. D. Cameron, and D. E. Russell. 1996. Estimating fat content of caribou from body condition scores. Journal of Wildlife Management 60:713–718.

Gluesing, E. A., and D. M. Field. 1986. Limitations of existing food-habit studies in modeling wildlife-habitat relationships. Pages 251–253 *in* J. Verner, M. L. Morrison, and C. J. Ralph, editors. Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. University of Wisconsin Press, Madison, Wisconsin, USA.

Graber, D. M., and M. White. 1983. Black bear food habits in Yosemite National Park. International Conference on Bear Research and Management 5:1–10.

Graber, D. M. 1990. Winter behavior of black bears in the Sierra Nevada, California. International Conference on Bear Research and Management 8:269–272.

Grogan, R. G., and F. G. Lindzey. 1999. Estimating population size of a low-density black bear population using capture-resight. Ursus 11:117–122.

Gunther, K. A., M. J. Biel, N. Anderson, and L. Waits. 2002. Probable grizzly bear predation on an American black bear in Yellowstone National Park. Ursus 13:372–374.

Hamilton, R. J., and R. L. Marchinton. 1980. Denning and related activities of black bears in the coastal plain of North Carolina. International Conference of Bear Research and Management 4:121–126.

Hanks, J. 2004. Characterization of population condition. Pages 47–73 *in* C. W. Fowler and T. D. Smith, editors. Dynamics of large mammal populations. The Blackburn Press, Caldwell, New Jersey, USA.

Hansen, J. A., S. L. Garman, B. Marks, and D. L. Urban. 1993. An approach for managing vertebrate diversity across multiple-use landscapes. Ecological Applications 3:481–496.

Harlow, H. J., T. Lohuis, T. D. I. Beck, and P. A. Iaizzo. 2001. Muscle strength in overwintering bears. Nature 409:997.

Harlow, H. J., T. Lohuis, R. G. Grogan, and T. D. I. Beck. 2002. Body mass and lipid changes by hibernating reproductive and nonreproductive black bears (*Ursus americanus*). Journal of Mammalogy 83:1020–1025.

Harms, D. R. 1980. Black bear management in Yosemite National Park. International Conference on Bear Research and Management 4:205–212.

Harris, R. B., and L. H. Metzgar. 1987. Harvest age structures as indicators of decline in small populations of grizzly bears. International Conference on Bear Research and Management 7:109–116.

Hatler, D. F. 1972. Food habits of black bears in interior Alaska. Canadian Field-Naturalist 86:17–31.

Hayes, S. G., and M. R. Pelton. 1994. Habitat characteristics of female black bear dens in northwestern Arkansas. International Conference on Bear Research and Management 9:411–418.

Hellgren, E. C. 1988. Ecology and physiology of a black bear (Ursus americanus) population in Great Dismal Swamp and reproductive physiology in the captive female black bear. Dissertation, Virginia Polytechnic Institute and State University, Blacksburg, Virginia, USA.

Hellgren, E. C. 1993. Status, distribution, and summer food habits of black bears in Big Bend National Park. The Southwestern Naturalist 38:77–80.

Hellgren, E. C., and D. S. Maehr. 1993. Habitat fragmentation and black bears in the eastern United States. Proceedings of the Eastern Workshop on Black Bear Research and Management 11:154–165.

Hellgren, E. C., L. L. Rogers, and U. S. Seal. 1993. Serum chemistry and hematology of black bears: physiological indices of habitat quality or seasonal patterns? Journal of Mammalogy 74:304–315.

Hellgren, E. C., and M. R. Vaughan. 1987. Home range and movements of winter-active black bears in the Great Dismal Swamp. International Conference on Bear Research and Management 7:227–234.

Hellgren, E. C., and M. R. Vaughan. 1988. Seasonal food habits of black bears in Great Dismal Swamp, Virginia-North Carolina. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 42:295–305.

Hellgren, E. C., and M. R. Vaughan. 1989. Denning ecology of black bears in a southeastern USA wetland. Journal of Wildlife Management 53:347–353.

Hellgren, E. C., and M. R. Vaughan. 1990. Range dynamics of black bears in Great Dismal Swamp, Virginia-North Carolina. Proceedings of the Annual Conference of Southeastern Association of Fish and Wildlife Agencies 44:268–278.

Hellgren, E. C., M. R. Vaughan, F. C. Gwazkauska, B. Williams, P. F. Scanlon, and R. L. Kirkpatrick. 1990. Endocrine and electrophoretic profiles during pregnancy and nonpregnancy in captive female black bears. Canadian Journal of Zoology 69:892–898.

Hellgren, E. C., M. R. Vaughan, and R. L. Kirkpatrick. 1989. Seasonal patterns in physiology and nutrition of black bears in Great Dismal Swamp, Virginia-North Carolina. Canadian Journal of Zoology 67:1837–1850.

Hellgren, E. C., M. R. Vaughan, and D. F. Stauffer. 1991. Macrohabitat use by black bears in a southeastern wetland. Journal of Wildlife Management 55:442–448.

Herrero, S. 1972. Aspects of evolution and adaptation in American black bears (*Ursus americanus* Pallas) and brown and grizzly bears (*Ursus actos* Linné) of North America. International Conference on Bear Research and Management 2:221–231.

Herrero, S. 1978. A comparison of some features of the evolution, ecology and behavior of black and grizzly/brown bears. Carnivore 1:7–17.

Herrero, S. 1983. Social behaviour of black bears at a garbage dump in Jasper National Park. International Conference on Bear Research and Management 5:54–70.

Herrero, S. 2002. Bear attacks-their causes and avoidance. The Lyons Press, Guilford, Connecticut, USA.

Hessl, A. E., and L. J. Graumlich. 2002. Interactive effects of human activities, herbivory and fire on quaking aspen (*Populus tremuloides*) age structures in western Wyoming. Journal of Biogeography 29:889–902.

Hewitt, D. G., and C. T. Robbins. 1996. Estimating grizzly bear food habits from fecal analysis. Wildlife Society Bulletin 24:547–550.

Hilderbrand, G. V., S. D. Farley, and C. T. Robbins. 1998. Predicting body condition of bears via two field methods. Journal of Wildlife Management 62:406–409.

Hilderbrand, G. V., C. C. Schwartz, C. T. Robbins, and T. A. Hanley. 2000. Effect of hibernation and reproductive status on body mass and condition of coastal brown bears. Journal of Wildlife Management 64:178–183.

Hirsch, J. G., L. C. Bender, and J. B. Haufler. 1999. Black bear, *Ursus americanus*, movements and home ranges on Drummond Island, Michigan. Canadian Field-Naturalist 113:221–225.

Hirsch, J. G., and J. B. Haufler. 1993. Evaluation of a forest habitat model for black bear. Proceedings of the International Union of Game Biologists 21:330–337.

Hirth, D. H., J. M. A. Petty, and C. W. Kilpatrick. 2002. Black bear, *Ursus americanus*, hair and apple trees, *Malus pumila*, in northeast North America. Canadian Field-Naturalist 116:305–307.

Hobbs, N. T., and D. M. Swift. 1985. Estimates of habitat carrying capacity incorporating explicit nutritional constraints. Journal of Wildlife Management 49:814–822.

Hock, R. J. 1960. Seasonal variation in physiological functions of arctic ground squirrels and black bears. Pages 155–171 *in* C. P. Lyman and A. R. Dawe, editors. Mammalian hibernation I. Harvard University, Cambridge, Massachusetts, USA.

Hoefs, M. E. G., and J. M. Shay. 1981. The effects of shade on shoot growth of *Vaccinium angustifolium* Ait. after fire pruning in southeastern Manitoba. Canadian Journal of Botany 59:166–174.

Horejsi, B. L., G. E. Hornbeck, and R. M. Raine. 1984. Wolves, *Canis lupus*, kill female black bear, *Ursus americanus*, in Alberta. Canadian Field-Naturalist 98:368–369.

Horner, M. A., and R. A. Powell. 1990. Internal structure of home ranges of black bears and analyses of home range overlap. Journal of Mammalogy 71:402–410.

Hugie, R. D. 1974. Habitat of the black bear in Maine. Eastern Workshop on Black Bear Management and Research 2:151–157.

Hugie, R. D. 1979. Working group report: central and northeast Canada and United States. Pages 250–271 *in* D. Burk, editor. The black bear in modern North America. Amwell Press, Clinton, New Jersey, USA.

Hugie, R. D. 1982. Black bear ecology and management in the northern conifer-deciduous forest of Maine. Dissertation, University of Montana, Missoula, Montana, USA.

Inman, R. M., and M. R. Pelton. 2002. Energetic production by soft and hard mast foods of American black bears in the Smoky Mountains. Ursus 13:57–68.

Irwin, L. L., and F. M. Hammond. 1985. Managing black bear habitats for food items in Wyoming. Wildlife Society Bulletin 13:477–483.

Johnson, D. D. P, W. Jetz, and D. W. Macdonald. 2002. Environmental correlates of badger social spacing across Europe. Journal of Biogeography 29:411–425.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Johnson, K. G., D. O. Johnson, and M. R. Pelton. 1978. Simulation of winter heat loss for a black bear in a closed tree den. Proceedings of the Eastern Black Bear Workshop 4:155–156.

Johnson, K. G., and M. R. Pelton. 1979. Denning behavior of black bears in the Great Smoky Mountains National Park. Proceedings of the Annual Conference of Southeastern Association of Fish and Wildlife Agencies 33:239–249.

Johnson, K. G., and M. R. Pelton. 1980. Environmental relationships and the denning period of black bears in Tennessee. Journal of Mammalogy 61:653–660.

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

Johnson, R. J., and F. D. Farrel. 1988. The prediction of body composition in poultry by estimation *in-vivo* of total body water with tritiated water and deuterium oxide. British Journal of Nutrition 59:109–124.

Jones, M. D., G. S. Warburton, and M. R. Pelton. 1998. Models for predicting occupied black bear habitat in coastal North Carolina. Ursus 10:203–207.

Jones, P. F., and R. J. Hudson. 2002. Winter habitat selection at three spatial scales by American elk, *Cervus elaphus*, in west-central Alberta. The Canadian Field-Naturalist 116:183–191.

Jonkel, C. 1978. Black, brown (grizzly) and polar bears. Pages 227–248 *in* J. L. Schmidt and D. L. Gilbert, editors. Big game of North America: ecology and management. Stackpole Books, Harrisburg, Pennsylvania, USA.

Jonkel, C. J., and I. McT. Cowan. 1971. The black bear in the spruce-fir forest. Wildlife Monographs 27.

Kane, D. M. 1989. Factors influencing the vulnerability of black bears to hunters in northern New Hampshire. Thesis, University of New Hampshire, Durham, New Hampshire, USA.

Kansas, J. L., and R. M. Raine. 1990. Methodologies used to assess the relative importance of ecological land classification units to black bears in Banff National Park, Alberta. International Conference on Bear Research and Management 8:155–160.

Kasbohm, J. W. 1994. Response of black bears to gypsy moth infestation in Shenandoah National Park, Virginia. Thesis, Virginia Polytechnic Institute and State University, Blacksburg, Virginia, USA.

Kasbohm, J. W., M. R. Vaughan, and J. G. Kraus. 1995. Food habits and nutrition of black bears during a gypsy moth infestation. Canadian Journal of Zoology 73:1771–1775.

Kasbohm, J. W., M. R. Vaughan, and J. G. Kraus. 1996. Effects of gypsy moth infestation on black bear reproduction and survival. Journal of Wildlife Management 60:408–416.

Kayser, C. 1961. The physiology of natural hibernation. Pergamon Press, New York, New York, USA.

Keay, J. A., and J. W. van Wagtendonk. 1983. Effect of Yosemite backcountry use levels on incidents with black bears. International Conference on Bear Research and Management 5:307–311.

Kelleyhouse, D. G. 1980. Habitat utilization by black bears in northern California. International Conference on Bear Research and Management 3:221–228.

Kemp, G. A. 1976. The dynamics and regulation of black bear *Ursus americanus* populations in northern Alberta. International Conference on Bear Research and Management 3:191–197.

Kemp, G. A. 1979. The Rocky Mountain working group. Pages 217–236 *in* D. Burk, editor. The black bear in modern North America. Amwell Press, Clinton, New York, USA.

Kendall, K. C. 1983. Use of pine nuts by grizzly and black bears in the Yellowstone area. International Conference on Bear Research and Management 5:166–173.

Kendall, K. C., L. H. Metzgar, D. A. Patterson, and B. M. Steele. 1992. Power of sign surveys to monitor population trends. Ecological Applications 2:422–430.

Kennedy, M., and R. D. Gray. 1993. Can ecological theory predict the distribution of foraging animals? A critical analysis of experiments on the Ideal Free Distribution. Oikos 68:158–166.

Kennedy, M. L., P. K. Kennedy, M. A. Bogan, and J. L. Waits. 2002. Geographic variation in the black bear (*Ursus americanus*) in the eastern United States and Canada. The Southwestern Naturalist 47:257–266.

Klenzendorf, S. A., M. R. Vaughan, and D. D. Martin. 2002. Den-type use and fidelity of American black bears in western Virginia. Ursus 13:39–44.

Knowlton, F. F., P. E. Martin, and J. C. Haug. 1968. A telemetric monitor for determining animal activity. Journal of Wildlife Management 32:943–948.

Koehler, G. M., and D. J. Pierce. 2003. Black bear home-range sizes in Washington: climatic, vegetative, and social influences. Journal of Mammalogy 84:81–91.

Kohlmann, S. G., R. L. Green, and C. E. Trainer. 1999. Effects of collection method on sex and age composition of black bear (*Ursus americanus*) harvest in Oregon. Northwest Science 73:34–38.

Kolenosky, G. B. 1986. The effects of hunting on an Ontario black bear population. International Conference on Bear Research and Management 6:45–55.

Kolenosky, G. B. 1990. Reproductive biology of black bears in east-central Ontario. International Conference on Bear Research and Management 8:385–392.

Kolenosky, G. B., and S. M. Strathearn. 1987. Winter denning of black bears in east-central Ontario. International Conference on Bear Research and Management 7:305–316.

Kotliar, N. B., and J. A. Wiens. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. Oikos 59:253–260.

Krebs, J. R., and N. B. Davies. 1993. An introduction to behavioural ecology. Third edition. Blackwell Scientific Publications, Oxford, United Kingdom.

Kushner, R. F. 1992. Bioelectrical impedance analysis: a review of principles and applications. Journal of the American College of Nutrition 11:199–209.

LaJeunesse, T. A., and R. O. Peterson. 1993. Marrow and kidney fat as condition indices in gray wolves. Wildlife Society Bulletin 21:87–90.

Landers, J. L., R. J. Hamilton, A. S. Johnson, and R. L. Marchinton. 1979. Foods and habitat of black bears in southeastern North Carolina. Journal of Wildlife Management 43:143–153.

Larivière, S., J. Huot, and C. Samson. 1994. Daily activity patterns of female black bears in a northern mixed-forest environment. Journal of Mammalogy 75:613–620.

Lawrence, W. 1979. Working group reports: Pacific working group: Habitat management and land use practices. Part 3. Pages 196–201 *in* D. Burk, editor. The black bear in modern North America. Amwell Press, Clinton, New York, USA.

LeCount, A. L. 1982. Population characteristics of Arizona black bears. Journal of Wildlife Management 46:861–868.

LeCount, A. L. 1983a. Denning ecology of black bears in central Arizona. International Conference on Bear Research and Management 5:71–78.

LeCount, A. L. 1983b. Evidence of wild black bears breeding while raising cubs. Journal of Wildlife Management 47:264–268.

LeCount, A. L. 1987. Causes of black bear cub mortality. International Conference on Bear Research and Management 7:75–82.

Lentz, W. M., R. L. Marchinton, and R. E. Smith. 1983. Thermodynamic analysis of northeastern Georgia black bear dens. Journal of Wildlife Management 47:545–550.

Lindzey, F. G., S. K. Thompson, and J. I. Hodges. 1977. Scent station index of black bear abundance. Journal of Wildlife Management 41:151–153.

Lindzey, F. G., and E. C. Meslow. 1976a. Characteristics of black bear dens on Long Island, Washington. Northwest Science 50:236–242.

Lindzey, F. G., and E. C. Meslow. 1976b. Winter dormancy in black bears in southwestern Washington. Journal of Wildlife Management 40:408–415.

Lindzey, F. G., and E. C. Meslow. 1977a. Population characteristics of black bears on an island in Washington. Journal of Wildlife Management 41:408–412.

Lindzey, F. G., and E. C. Meslow. 1977b. Home range and habitat use by black bears in southwestern Washington. Journal of Wildlife Management 41:413–425.

Lindzey, J. S., G. L. Alt, C. R. McLaughlin, and W. S. Kordek. 1983. Population response of Pennsylvania black bears to hunting. International Conference on Bear Research and Management 5:34–39.

Lindzey, J. S., W. S. Kordek, G. J. Matula, Jr., and W. P. Piekielek. 1976. The black bear in Pennsylvania—status, movements, values, and management. International Conference on Bear Research and Management 3:215–224.

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.

Litvaitis, J. A., and D. M. Kane. 1994. Relationship of hunting techniques and hunter selectivity to composition of black bear harvest. Wildlife Society Bulletin 22:604–606.

Lofroth, E. C. 1993. Scale dependent analysis of habitat selection by marten in the sub-boreal spruce biogeoclimatic zone. Thesis, Simon Fraser University, Burnaby, British Columbia, Canada.

Lord, J. M., and D. H. Norton. 1990. Spatial scale and the concept of fragmentation. Conservation Biology 4:197–202.

Lundberg, D. A., R. A. Nelson, H. W. Wahner, and J. P. Jones. 1976. Protein metabolism in the black bear before and during hibernation. Mayo Clinic Proceedings 51:716–722.

Lyons, A. L., W. L. Gaines, and C. Servheen. 2003. Black bear resource selection in the northeast Cascades, Washington. Biological Conservation 113:55–62.

Lyman, C. P., J. S. Willis, A. Malan, L. C. H. Wang. 1982. Hibernation and torpor in mammals and birds. Academic Press, New York.

MacDonald, D. W., P. D. Stewart, P. Stopka, and N. Yamaguchi. 2000. Measuring the dynamics of mammalian societies: an ecologist's guide to ethological methods. Pages 332–388 *in* L. Boitani and T. K. Fuller, editors. Research techniques in animal ecology: controversies and consequences. Columbia University Press, New York, New York, USA.

MacHutchon, A. G. 1989. Spring and summer food habits of black bears in the Pelly River Valley, Yukon. Northwest Science 63:116–118.

MacHutchon, A. G. 2001. Grizzly bear activity budget and pattern in the Firth River Valley, Yukon. Ursus 12:189–198.

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

MacNab, W. H. 1993. A topographic index to quantify the effect of mesoscale landform on site productivity. Canadian Journal of Forest Research 23:100–107.

Maehr, D. S. 1984. Distribution of black bears in eastern North America. Proceedings of the Eastern Workshop on Black Bear Research and Management 7:74.

Maehr, D. S., J. N. Layne, E. D. Land, J. W. McCown, and J. C. Roof. 1988. Long distance movements of a Florida black bear. Florida Field Naturalist 16:1–6.

Maher, C. R. 1994. Pronghorn male spatial organization: population differences in degree of nonterritoriality. Canadian Journal of Zoology 72:455–464.

Maher, C. R., and D. F. Lott. 2000. A review of ecological determinants of territoriality within vertebrate species. American Midland Naturalist 143:1–29.

Manville, A. M., II. 1983. Human impact on the black bear in Michigan’s lower peninsula. International Conference on Bear Research and Management 5:20–33.

Manville, A. M., II. 1987. Den selection and use by black bears in Michigan’s northern lower peninsula. International Conference on Bear Research and Management 7:317–322.

Martorello, D. A., T. H. Eason, and M. R. Pelton. 2001. A sighting technique using cameras to estimate population size of black bears. Wildlife Society Bulletin 29:560–567.

Martorello, D. A., and M. R. Pelton. 2003. Microhabitat characteristics of American black bear nest dens. Ursus 14:21–26.

Massopust, J. L. 1984. Black bear homing tendencies, response to being chased by hunting dogs, reproductive biology, denning behavior, home range, diel movements, and habitat use in northern Wisconsin. Thesis, University of Wisconsin at Stevens Point, Stevens Point, Wisconsin, USA.

Matthews, N., and W. Porter. 1988. Black bear predation on white-tailed deer neonates in the central Adirondacks. Canadian Journal of Zoology 66:1241–1242.

Mattson, D. J. 1990. Human impacts on bear habitat use. International Conference on Bear Research and Management 8:33–56.

Mattson, D. J. 2001. Myrmecophagy by Yellowstone grizzly bears. Canadian Journal of Zoology 79:779–793.

Mattson, D. J., R. R. Knight, and B. M. Blanchard. 1992. Cannibalism and predation on black bears by grizzly bears in Yellowstone ecosystem, 1975–1990. Journal of Mammalogy 73:422–425.

Maxwell, R. K., L. L. Rogers, and R. B. Brander. 1972. The energetics of wintering bears (*Ursus americanus*) in northeastern Minnesota (abstract). Bulletin of the Ecological Society of America 53:21. (Abstract)

Maxwell, R. K., J. Thorkelson, and L. L. Rogers. 1988. The field energetics of winter-dormant black bear (*Ursus americanus*) in northeastern Minnesota. Canadian Journal of Zoology 66:2095–2103.

McCall, T. C., R. D. Brown, and L. C. Bender. 1997. Comparison of techniques for determining the nutritional carrying capacity for white-tailed deer. Journal of Range Management 50:33–38.

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.

McCutchen, H. E. 1993. Ecology of high mountain black bear population in relation to land use at Rocky Mountain NP. Park Science 13:25–27.

McDonald, J. E., and T. K. Fuller. 1998. Testing assumptions in bear research: using statistical power analysis to estimate effects of den type on black bear cub survival. Ursus 10:405–411.

McDonald, J. E., Jr., and T. K. Fuller. 2001. Prediction of litter size in American black bears. Ursus 12:93–102.

McDonald, J. E., Jr., D. P. Fuller, T. K. Fuller, and J. E. Cardoza. 1994. The influence of food abundance on success of Massachusetts black bear hunters. Northeast Wildlife 51:55–60.

McLaughlin, C. R., G. J. Matula, Jr., and R. J. O'Connor. 1994. Synchronous reproduction by Maine black bears. International Conference on Bear Research and Management 9:471–479.

McLean, P. K., and M. R. Pelton. 1990. Some demographic comparisons of wild and panhandler bears in the Smoky Mountains. International Conference on Bear Research and Management 8:105–112.

McLellan, B. N., and D. M. Shackleton. 1988. Grizzly bears and resource-extraction industries: effects of roads on behavior, habitat use and demography. Journal of Applied Ecology 25:451–460.

McLoughlin, P. D., S. H. Ferguson, and F. Messier. 2000. Intraspecific variation in home range overlap with habitat quality: a comparison among brown bear populations. Evolutionary Ecology 14:39–60.

Mealey, S. P. 1975. The natural food habits of free-ranging grizzly bears in Yellowstone National Park, 1973–1974. Thesis, Montana State University, Bozeman, Montana, USA.

Messier, F., J. A. Virgl, and L. Marinelli. 1990. Density-dependent habitat selection in muskrats: a test of the ideal free distribution model. Oecologia 84:380–385.

Miller, D. A., B. D. Leopold, and H. A. Jacobson. 1995. Use of bait stations to monitor black bear populations in the Mississippi alluvial valley. Southeastern Association of Fish and Wildlife Agencies 49:560–569.

Miller, S. D., E. F. Becker, and W. B. Ballard. 1987. Black and brown bear density estimates using modified capture-recapture techniques in Alaska. International Conference on Bear Research and Management 7:23–35.

Miller, S. D., and V. L. Tutterrow. 1999. Characteristics of nonsport mortalities to brown and black bears and human injuries from bears in Alaska. Ursus 11:239–252.

Miller, S. D., G. C. White, R. A. Sellers, H. V. Reynolds, J. W. Schoen, K. Titus, V. G. Barnes, Jr., T. B. Smith, R. R. Nelson, W. B. Ballard, and C. C. Schwartz. 1997. Brown and black bear density estimation in Alaska using radiotelemetry and replicated mark-resight techniques. Wildlife Monographs 133.

Mitchell, M. S., and R. A. Powell. 2003. Response of black bears to forest management in the southern Appalachian Mountains. Journal of Wildlife Management 67:692–705.

Mitchell, M. S., J. W. Zimmerman, and R. A. Powell. 2002. Test of a habitat suitability index for black bears in the southern Appalachians. Wildlife Society Bulletin 30:794–808.

Mollohan, C., W. W. Brady, and A. L. LeCount. 1989. Habitat use of an Arizona ponderosa pine-mixed conifer forest by female black bears. Western Journal of Applied Forestry 4:6–10.

Morrison, M. L., B. G. Marcot, and R. W. Mannan. 1992. Wildlife-habitat relationships: concepts and applications. First edition. The University of Wisconsin Press, Madison, Wisconsin, USA.

Moruzzi, T. L., T. K. Fuller, R. M. DeGraaf, R. T. Brooks, and W. Li. 2002. Assessing remotely triggered cameras for surveying carnivore distribution. Wildlife Society Bulletin 30:380–386.

Murphy, M. A., L. P. Waits, and K. C. Kendall. 2000. Quantitative evaluation of fecal drying methods for brown bear DNA analysis. Wildlife Society Bulletin 28:951–957.

Mykytka, J. M., and M. R. Pelton. 1990. Management strategies for Florida black bears based on home range habitat composition. International Conference on Bear Research and Management 8:161–167.

Mysterud, A., P. K. Larsen, R. A. Ims, and E. østbye. 1999. Habitat selection by roe deer and sheep: does habitat ranking reflect resource availability? Canadian Journal of Zoology 77:776–783.

National Park Service. 1988. Management policies. U. S. Department of the Interior, Washington D. C., USA.

Nelson, O. L., M-M McEwen, C. T. Robbins, L. Felicetti, and W. F. Christensen. 2003. Evaluation of cardiac function in active and hibernating grizzly bears. Journal of the American Veterinary Medical Association 223:1170–1175.

Nelson, R. A. 1980. Protein and fat metabolism in hibernating bears. Federation Proceedings 39:2955–2958.

Nelson, R. A., G. E. Folk, Jr., R. D. Feld, and P. Ringens. 1979. Biochemical transition from hibernation to normal activity in bears (abstract). Federation Proceedings 38:1227. (Abstract)

Nelson, R. A., G. E. Folk, Jr., E. W Pfeiffer, J. J. Craighead, C. J. Jonkel, and D. L. Steiger. 1983. Behavior, biochemistry, and hibernation in black, grizzly, and polar bears. International Conference on Bear Research and Management 5:284–290.

Nelson, R. A., J. D. Jones, H. W. Wahner, D. B. McGill, and C. F. Code. 1975. Nitrogen metabolism in bears: urea metabolism in summer starvation and in winter sleep and role of urinary bladder in water and nitrogen concentration. Mayo Clinic Proceedings 50:141–146.

Nelson, R. A., H. W. Wahner, J. D. Jones, R. D. Ellefson, and P. E. Zollman. 1973. Metabolism of bears before, during, and after winter sleep. American Journal of Physiology 224:491–496.

Northcott, T. H., and F. E. Elsey. 1971. Fluctuations in black bear populations and their relationship to climate. Canadian Field-Naturalist 85:123–128.

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.

Noyce, K. V., and P. L. Coy. 1990. Abundance and productivity of bear food species in different forest types of northcentral Minnesota. International Conference on Bear Research and Management 8:169–181.

Noyce, K. V., P. L. Coy, and D. L. Garshelis. 2002. Bone prominence and skin-fold thickness as predictors of body fat and reproduction in American black bears. Ursus 13:275–284.

Noyce, K. V., and D. L. Garshelis. 1994. Body size and blood characteristics as indicators of condition and reproductive performance in black bears. International Conference on Bear Research and Management 9:481–496.

Noyce, K. V., D. L. Garshelis, and P. L. Coy. 2001. Differential vulnerability of black bears to trap and camera sampling and resulting biases in mark-recapture estimates. Ursus 12:211–226.

Noyce, K. V., P. B. Kannowski, and M. R. Riggs. 1997. Black bears as ant-eaters: seasonal associations between bear myrmecophagy and ant ecology in north-central Minnesota. Canadian Journal of Zoology 75:1671–1686.

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.

Oli, M. K., H. A. Jacobson, and B. D. Leopold. 2002. Pattern of space use by female black bears in the White River National Wildlife Refuge, Arkansas, USA. Journal for Nature Conservation 10:87–93.

O’Neill, R. V., B. T. Milne, M. G. Turner, and R. H. Gardner. 1988. Resource utilization scales and landscape pattern. Landscape Ecology 2:63–69.

O’Pezio, J., S. H. Clarke, and C. Hackford. 1983. Chronology of black bear denning in the Catskill region of New York. International Conference on Bear Research and Management 5:87–94.

Otto, K. L., J. D. Ferguson, D. G. Fox, and C. J. Sniffen. 1991. Relationship between body condition score and composition of ninth to eleventh rib tissue in Holstein dairy cows. Journal of Dairy Science 74:852–859.

Parker, G. G. 1995. Structure and microclimate of forest canopies. Pages 73–106 *in* M. D. Lowman and N. M. Nadkarni, editors. Forest Canopies. Academic Press, San Diego, California, USA.

Partridge, S. T., D. L. Nolte, G. J. Zielgltrum, and C. T. Robbins. 2001. Impacts of supplemental feeding on the nutritional ecology of black bears. Journal of Wildlife Management 65:191–199.

Payne, N. F., B. E. Kohn, N. C. Norton, and G. G. Bertagnoli. 1998. Black bear food items in northern Wisconsin. Transactions of the Wisconsin Academy of Sciences, Arts and Letters 86:263–280.

Pearson, A. M. 1975. The northern interior grizzly bear (*Ursus arctos* L.). Canadian Wildlife Service Report Series Number 34.

Pedlar, J. H., L. Fahrig, and H. G. Merriam. 1997. Raccoon habitat use at 2 spatial scales. Journal of Wildlife Management 61:102–112.

Pelchat, B. O., and R. L. Ruff. 1986. Habitat and spatial relationships of black bears in boreal mixedwood forest of Alberta. International Conference on Bear Research and Management 6:81–92.

Pelton, M. R. 1972. Use of foot trail travelers in the Great Smoky Mountains National Park to estimate black bear (*Ursus americanus*) activity. International Conference on Bear Research and Management 2:36–42.

Pelton, M. R. 1989. The impact of oak mast on black bears in the southern Appalachians. Pages 7–11 *in* C. E. McGee, editor. Southern Appalachian mast management. University of Tennessee, Knoxville, Tennessee, USA.

Pelton, M. R. 2000. Black bear. Pages 389–408 *in* S. Demarais and P. R. Krausman, editors. Ecology and management of large mammals in North America. Prentice-Hall, Inc., Upper Saddle River, New Jersey, USA.

Pelton, M. R. 2003. Black bear (*Ursus americanus*). Pages 547–555 *in* G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, editors. Wild mammals of North America: biology, management, and conservation. Second edition, revised. The Johns Hopkins University Press, Baltimore, Maryland, USA.

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

Pelton, M. R., A. B. Coley, T. H. Eason, D. L. Doan Martinez, J. A. Pederson, F. T. van Manen, and K. M. Weaver. 1999. American black bear conservation action plan. Pages 144–156 *in* C. Servheen, S. Herrero, and B. Peyton, editors. Bears: status survey and conservation action plan. International Union for the Conservation of Nature, Species Survival Commission Bear Specialist Group, Gland, Switzerland, and Cambridge, UK.

Pelton, M. R., and F. T. van Manen. 1994. Distribution of black bears in North America. Proceedings of the Eastern Workshop on Black Bear Research and Management 12:133–138.

Pelton, M. R., and F. T. van Manen. 1996. Benefits and pitfalls of long-term research: a case study of black bears in Great Smoky Mountains National Park. Wildlife Society Bulletin 24:443–450.

Poelker, R. J., and H. D. Hartwell. 1973. Black bear of Washington. Washington State Game Department. Biological Bulletin 14.

Powell, R. A. 1987. Black bear home range overlap in North Carolina and the concept of home range applied to black bears. International Conference on Bear Research and Management 7:235–242.

Powell, R. A. 2000. Animal home ranges and territories and home range estimators. Pages 65–110 *in* L. Boitani and T. K. Fuller, editors. Research techniques in animal ecology. Columbia University Press, New York, New York, USA.

Powell, R. A., J. W. Zimmerman, and D. E. Seaman. 1997. Ecology and behavior of North American black bears: home ranges, habitat and social organization. Chapman and Hall, London, United Kingdom.

Powell, R. A., J. W. Zimmerman, D. E. Seaman, and J. F. Gilliam. 1996. Demographic analysis of a hunted black bear population with access to a refuge. Conservation Biology 10:224–234.

Pritchard, G. T., and C. T. Robbins. 1990. Digestive and metabolic efficiencies of grizzly and black bears. Canadian Journal of Zoology 68:1645–1651.

Pullium, H. R. 1996. Sources and sinks: empirical evidence and population consequences. Pages 45–69 *in* O. E. Rhodes, Jr., R. K. Chesser, and M. H. Smith, editors. Population dynamics in ecological space and time. University of Chicago Press, Chicago, Illinois, USA.

Raine, R. M., and J. L. Kansas. 1990. Black bear seasonal food habits and distribution by elevation in Banff national Park, Alberta. International Conference on Bear Research and Management 8:297–304.

Rausch, R. L. 1961. Notes on the black bear (*Ursus americanus* Pallus) in Alaska with particular reference to dentition and growth. Zeitschrift fur Sangetierkunk 26:77–107.

Reimchen, T. E. 1998. Nocturnal foraging behaviour of black bears, *Ursus americanus*, on Moresby Island, British Columbia. Canadian Field-Naturalist 112:446–450.

Reynolds, D. G., and J. J. Beecham. 1980. Home range activities and reproduction of black bears in west-central Idaho. International Conference of Bear Research and Management 4:181–190.

Reynolds, H. V., J. A. Curatolo, and R. Quimby. 1976. Denning ecology of grizzly bears in northeastern Alaska. International Conference of Bear Research and Management 3:403–409.

Rice, C. G., J. Rohlman, J. Beecham, and S. Pozzanghera. 2001. Power analysis of bait station surveys in Idaho and Washington. Ursus 12:227–236.

Ritchie, M. E. 1998. Scale-dependent foraging and patch choice in fractal environments. Evolutionary Ecology 12:309–330.

Robbins, C. T. 1973. The biological basis for the determination of carrying capacity. Dissertation, Cornell University, Ithaca, New York, USA.

Robbins, C. T. 1993. Wildlife feeding and nutrition. Second edition. Academic Press, San Diego, California, USA.

Rode, K. D., and C. T. Robbins. 2000. Why bears consume mixed diets during fruit abundance. Canadian Journal of Zoology 78:1640–1645.

Rogers, L. L. 1976. Effects of mast and berry crop failures on survival, growth, and reproductive success of black bears. Transactions of the North American Wildlife and Natural Resource Conference 41:431–438.

Rogers, L. L. 1977. Social relationships, movements, and population dynamics of black bears in northeastern Minnesota. Dissertation, University of Minnesota, Minneapolis, Minnesota, USA.

Rogers, L. L. 1980. Inheritance of coat color and changes in pelage coloration in black bears in northeastern Minnesota. Journal of Mammalogy 61:324–327.

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.

Rogers, L. L. 1993. The role of habitat quality in the natural regulation of black bear populations. Proceedings of the Western Black Bear Conference 4:95–102.

Rogers, L. L., and A. W. Allen. 1987. Habitat suitability index models: black bear, Upper Great Lakes Region. U. S. Fish and Wildlife Services Biological Report 82.

Rogers, L. L., D. W. Kuehn, A. W. Erickson, E. M. Harger, L. J. Verme, and J. J. Ozoga. 1976. Characteristics and management of black bears that feed in garbage dumps, campgrounds or residential areas. International Conference on Bear Research and Management 3:169–175.

Rogers, L. L., and L. D. Mech. 1981. Interactions of wolves and black bears in northeastern Minnesota. Journal of Mammalogy 62:434–436.

Rogers, L. L., and S. M. Rogers. 1976. Parasites of bears: a review. International Conference on Bear Research and Management 3:411–430.

Rogers, L. L., and G. A. Wilker. 1987. Researcher-conditioned black bears provide detailed habitat use data (abstract). Pages 177–178 *in* Abstracts of the 49th Midwest Fish and Wildlife Conference. December 5–9, 1987. Milwaukee, Wisconsin, USA. (Abstract)

Rogers, L. L., G. A. Wilker, and A. W. Alien. 1988. Managing northern forests for black bears. Pages 36–42 *in* T. W. Hoekstra and J. Capp, editors. Integrating forest management for wildlife and fish. U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station, General Technical Report NC-122.

Roloff, G. J., and B. J. Kernohan. 1999. Evaluating the reliability of habitat suitability index models. Wildlife Society Bulletin 27:973–985.

Roof, J. C. 1997. Black bear food habits in the lower Wekiva River Basin of central Florida. Florida Field Naturalist 25:92–97.

Rosenzweig, M. L. 1968. Net primary production of terrestrial communities: prediction from climatological data. American Naturalist 102:67–74.

Roth, H. U. 1983. Diel activity of a remnant population of European brown bears. International Conference on Bear Research and Management 5:223–229.

Roth, H. U., and D. Huber. 1986. Diel activity of brown bears in Plitvice Lakes National Park, Yugoslavia. International Conference on Bear Research and Management 6:177–181.

Rounds, R. C. 1987. Distribution and analysis of colour morphs of the black bear (*Ursus americanus*). Journal of Biogeography 14:521–538.

Ruby, N. F. 2003. Hibernation: when good clocks go cold. Journal of Biological Rhythms 18:275–286.

Ruby, N. F., J. Dark, D. E. Burns, H. C. Heller, and I. Zucker. 2002. The suprachiasmatic nucleus is essential for circadian body temperature rhythms in hibernating ground squirrels. Journal of Neuroscience 22:357–364.

Russel, A. J. F., J. M. Doney, and R. G. Gunn. 1969. Subjective assessment of body fat in live sheep. Journal of Agricultural Science 72:451–-454.

Samson, C., and J. Huot. 1995. Reproductive biology of female black bears in relation to body mass in early winter. Journal of Mammalogy 76:68–77.

Samson, C., and J. Huot. 1998. Movements of female black bears in relation to landscape vegetation type in southern Québec. Journal of Wildlife Management 62:718–727.

Samson, C., and J. Huot. 2001. Spatial and temporal interactions between female American black bears in mixed forests of eastern Canada. Canadian Journal of Zoology 79:633–641.

Sargeant, G. A., and R. L. Ruff. 2001. Demographic response of black bears at Cold Lake, Alberta, to the removal of adult males. Ursus 12:59–68.

Schenk, A., M. E. Obbard, and K. M. Kovacs. 1998. Genetic relatedness and home-range overlap among female black bears (*Ursus americanus*) in northern Ontario, Canada. Canadian Journal of Zoology 76:1511–1519.

Schoen, J. W. 1990. Bear habitat management: a review and future perspective. International Conference on Bear Research and Management 8:143–154.

Schoen, J. W., L. R. Beier, J. W. Lentfer, and L. J. Johnson. 1987. Denning ecology of brown bears on Admiralty and Chichagof islands. International Conference on Bear Research and Management 7:293–304.

Schooley, R. L., C. R. McLaughlin, W. B. Krohn, and G. J. Matula, Jr. 1994a. Spatiotemporal patterns of macrohabitat use by female black bears during fall. International Conference on Bear Research and Management 9:339–348.

Schooley, R. L., C. R. McLaughlin, G. J. Matula, Jr. and W. B. Krohn. 1994b. Denning chronology of female black bears: effects of food, weather, and reproduction. Journal of Mammalogy 75:466–477.

Schorger, A. W. 1949. The black bear in early Wisconsin. Transactions of the Wisconsin Academy of Science, Arts, and Letters 39:151–194.

Schroeder, M. T. 1987. Blood chemistry, hematology, and condition evaluation of black bears in northcoastal California. International Conference on Bear Research and Management 7:333–349.

Schwartz, C. C., and A. W. Franzmann. 1991. Interrelationship of black bears to moose and forest succession in the northern coniferous forest. Wildlife Monographs 113.

Schwartz, C. C., and A. W. Franzmann. 1992. Dispersal and survival of subadult black bears from the Kenai Peninsula, Alaska. Journal of Wildlife Management 56:426–431.

Schwartz, C. C., S. D. Miller, and A. W. Franzmann. 1987. Denning ecology of three black bear populations in Alaska. International Conference on Bear Research and Management 7:281–291.

Scott, M. G. 1991. Body fat prediction, nutrition and reproduction of black bears in the interior highlands of Arkansas. Thesis, University of Arkansas, Fayetteville, Arkansas, USA.

Singer, F. J., and S. P. Bratton. 1980. Black bear/human conflicts in the Great Smoky Mountains National Park. International Conference on Bear Research and Management 4:137–139.

Skinner, M. P. 1925. Bears in Yellowstone. A. C. McClurgand Company, Chicago, Illinois, USA.

Smith, B. E. 1946. Bear facts. Journal of Mammalogy 27:31–37.

Smith, D. W., D. R. Trauba, R. K. Anderson, and R. O. Peterson. 1994a. Black bear predation on beavers on an island in Lake Superior. American Midland Naturalist 132:248–255.

Smith, M. E., J. L. Hechtel, and E. H. Follmann. 1994b. Black bear denning ecology in interior Alaska. International Conference on Bear Research and Management 9:513–522.

Smith, T. R. 1985. Ecology of black bears in the bottomland hardwood forest in Arkansas. Dissertation, University of Tennessee, Knoxville, Tennessee, USA.

Stephenson, T. R., K. J. Hundertmark, C. C. Schwartz, and V. Van Ballenberghe. 1998. Predicting body fat and body mass in moose with ultrasonography. Canadian Journal of Zoology 76:717–722.

Stephenson, T. R., V. C. Bleich, B. M. Pierce, and G. P. Mulcahy. 2002. Validation of mule deer body composition using *in vivo* and post-mortem indices of nutritional condition. Wildlife Society Bulletin 30:557–564.

Sternberg, M., and M. Shoshany. 2001. Influence of slope aspect on Mediterranean woody formations: comparison of a semiarid and an arid site in Israel. Ecological Research 16:335–345.

Stirling, I., and A. E. Derocher. 1990. Factors affecting the evolution and behavioral ecology of the modern bears. International Conference on Bear Research and Management 8:189–204.

Stratman, M. R., C. D. Alden, M. R. Pelton, and M. E. Sunquist. 2001a. Habitat use by American black bears in the sandhills of Florida. Ursus 12:109–114.

Stratman, M. R., C. D. Alden, M. R. Pelton, and M. E. Sunquist. 2001b. Long distance movement of a Florida black bear in the southeastern coastal plain. Ursus 12:55–58.

Stringham, S. F. 1986. Effects of climate, dump closure, and other factors on Yellowstone grizzly bear litter size. International Conference on Bear Research and Management 6:33–39.

Stringham, S. F. 1990. Black bear reproductive rate relative to body weight in hunted populations. International Conference on Bear Research and Management 8:425–432.

Stubblefield, C. H. 1993. Food habits of black bear in the San Gabriel Mountains of southern California. The Southwestern Naturalist 38:290–293.

Swenson, J. E., A. Jansson, R. Riig, and F. Sandegren. 1999. Bears and ants: myrmecophagy by brown bears in central Scandinavia. Canadian Journal of Zoology 77:551–561.

Swenson, J. E., W. F. Kasworm, S. T. Stewart, C. A. Simmons, and K. Aune. 1987. Interpopulation applicability of equations to predict live weight in black bears. International Conference on Bear Research and Management 7:359–362.

Tate, J., and M. R. Pelton. 1983. Human-bear interactions in Great Smoky Mountains National Park. International Conference on Bear Research and Management 5:312–321.

Taylor, M. 1994. Density-dependent population regulation in black, brown, and polar bears. International Conference on Bear Research and Management Monograph Series 3.

Taylor, M. K., D. P. DeMaster, G. L. Bunnell, and R. E. Schweinsburg. 1987. Modeling the sustainable harvest of female polar bears. Journal of Wildlife Management 51:811–820.

Tietje, W. D., B. O. Pelchat, and R. L. Ruff. 1986. Cannibalism of denned black bears. Journal of Mammalogy 67:762–766.

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.

Tinker, D. B., H. J. Harlow, and T. D. I. Beck. 1998. Protein use and muscle-fiber changes in free-ranging, hibernating black bears. Physiological Zoology 71:414–424.

Valdmann, H., U. Saarma, and A. Karis. 2001. The brown bear population in Estonia: current status and requirements for management. Ursus 12:31–36.

van Manen, R. T. 1994. Black bear habitat use in Great Smoky Mountains National Park. Dissertation, University of Tennessee, Knoxville, Tennessee, USA.

van Manen, R. T., and M. R. Pelton. 1997. A GIS model to predict black bear habitat use. Journal of Forestry 95:6–12.

Van Why, K. R., and M. J. Chamberlain. 2003. Mortality of black bears, *Ursus americanus*, associated with elevated train trestles. Canadian Field-Naturalist 117:113–115.

Waddell, T. 1979. State and provincial status reports: Arizona. Pages 33–37 *in* A. LeCount, editor. First western black bear workshop. Tempe, Arizona, USA.

Wagner, R. O., D. A. Hightower, and R. M. Pace. 2001. Measuring levels and patterns of activity in black bears. Ursus 12:181–188.

Wathen, W. G., K. G. Johnson, and M. R. Pelton. 1986. Characteristics of black bear dens in the southern Appalachian region. International Conference on Bear Research and Management 6:119–127.

Watts, P. D., N. A. Oritsland, C. Jonkel, and K. Ronald. 1981. Mammalian hibernation and the oxygen consumption of a denning black bear (*Ursus americanus*). Comparative Biochemistry and Physiology A Comparative Physiology 69:121–123.

Weaver, K., and M. R. Pelton. 1994. Denning ecology of black bears in the Tensas River Basin of Louisiana. International Conference on Bear Research and Management 9:427–433.

Weir, R. D., and A. S. Harestad. 2003. Scale-dependent habitat selectivity by fishers in south-central British Columbia. Journal of Wildlife Management 67:73–82.

Welch, C. A., J. Keay, K. C. Kendall, and C. T. Robbins. 1997. Constraints on frugivory by bears. Ecology 78:1105–1119.

Wertz, T. L., J. J. Akenson, M. G. Henjum, and E. L. Bull. 2001. Home range and dispersal patterns of subadult black bears in northeastern Oregon. Western Black Bear Workshop 7:93–100.

White, G. C., and R. A. Garrott. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, California, USA.

White, T. H., Jr., J. L. Bowman, H. A. Jacobson, B. D. Leopold, and W. P. Smith. 2001. Forest management and female black bear denning. Journal of Wildlife Management 65:34–40.

Whittaker, R. H. 1975. Communities and ecosystems. Second edition, Macmillan, New York, New York, USA.

Wielgus, R. B., F. Sarrazin, R. Ferriere, and J. Clobert. 2001. Estimating effects of adult male mortality on grizzly bear population growth and persistence using matrix models. Biological Conservation 98:293–303.

Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology 3:385–397.

Wimsatt, W. A. 1963. Delayed implantation in the Ursidae, with particular reference to the black bear. Pages 49–76 *in* A. C. Ender, editor. Delayed implantation. University of Chicago Press, Chicago, Illinois, USA.

With, K. A. 1994. Using fractal analysis to assess how species perceive landscape structure. Landscape Ecology 9:25–36.

Wolff, J. O. 1997. Population regulation in mammals: an evolutionary perspective. Journal of Animal Ecology 66:1–13.

Wolff, J. O., and J. A. Peterson. 1998. An offspring-defense hypothesis for territoriality in female mammals. Ethology Ecology & Evolution 10:227–239.

Wooding, J. B., and J. R. Brady. 1987. Black bear road-kills in Florida. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 41:438–442.

Wooding, J. B., and T. S. Hardisky. 1992. Black bear denning in northcentral Florida. Journal of Mammalogy 73:895–898.

Wooding, J. B., and T. S. Hardisky. 1994. Home range, habitat use, and mortality of black bears in north-central Florida. International Conference on Bear Research and Management 9:349–356.

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

Young, B. F., and R. L. Ruff. 1982. Population dynamics and movements of black bears in east central Alberta. Journal of Wildlife Management 46:854–860.

Zardus, M. J., and D. J. Parsons. 1980. Black bear management in Sequoia and Kings Canyon National Parks. International Conference on Bear Research and Management 4:195–200.

Zar, J. H. 1999. Biostatistical analysis. Third edition. Prentice-Hall, Englewood Cliffs, New Jersey, USA.

Zeigenfuss, L. C. 2001. Ecology of black bears in Rocky Mountain National Park: an analysis of population dynamics, diet, and habitat selection (1985–1991). Unpublished report, U.S. National Park Service, Rocky Mountain National Park, Colorado, USA.

Zimmerman, J. W. 1992. A habitat suitability index model for black bears in the southern Appalachian region evaluated with location error. Dissertation, North Carolina State University, Raleigh, North Carolina, USA.