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Survival and productivity of a low-density black bear population in Rocky Mountain National Park, Colorado

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Abstract: Historically, Rocky Mountain National Park (RMNP) has supported a small black bear (*Ursus americanus*) population of low productivity. Increased visitor use of the park and development around its periphery could lead to a reduction in population viability of RMNP's bear population or could increase the potential for human–bear conflict. Therefore, we investigated contemporary survival and productivity parameters for RMNP's black bear population from 2003 to 2006 and compared these values to historic levels (1984–1991) and population means throughout the western United States to clarify the current status of RMNP's bear population. The contemporary black bear population showed signs of earlier reproduction and higher cub survival when compared to historic bears; litter size and adult and subadult survival were similar between contemporary and historic periods. Increased productivity of the contemporary population was likely due to better nutritional condition of reproductive females, which showed significantly higher body condition index scores, body fat, and weights, which are likely due to observed greater use of anthropogenic food sources. The population of black bears in RMNP may have greater growth potential than was observed historically, decreasing the reliance on immigration from adjacent populations. However, increased human–bear conflicts associated with greater use of human-associated habitats in RMNP may negate some of the advantages of increased population productivity because of removal of problem bears.

Key words: black bear, Colorado, human–bear conflicts, human–wildlife conflicts, Rocky Mountain National Park, *Ursus americanus*

Fewer than 25 black bears (*Ursus americanus*; Baldwin 2008) exist in Rocky Mountain National Park (RMNP). This is likely due to limited natural food sources. 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. Given RMNP's low density and the relatively low reproductive output of black bears, it is important to monitor this population to assess potential changes in population size and factors influencing these changes.

Common causes of mortality for subadult and adult black bears include intra- and inter-specific predation, starvation, old age, and legal and illegal harvest (LeCount 1987, Pelton 2000, Pelton 2003, Beckmann and Lackey 2008, Cotton 2008). Neonate and yearling survival is influenced by habitat quality, spring nutrition, experience of the mother, weather, predator numbers (including conspecifics), and mast abundance in autumn (LeCount 1987, Rogers 1987, 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 (McCutchen 1993, Noyce and Garshelis 1994). Similarly, most reproductive parameters of black bears (i.e., age of primiparity, litter size, interbirth interval) are influenced by maternal size and condition (Rogers 1987, Elowe and Dodge 1989, Beckmann and Berger 2003, Costello et al. 2003), although the effect varies with the absolute condition of bears (Noyce and Garshelis 1994). For example, litter size is greatest at highest levels of condition, but rapidly declines to a stable level of 1 to 2 cubs per litter (Noyce and Garshelis 1994). Age of primiparity is lower for females in good condition, and thus can have

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a strong influence on overall productivity of both the individual and the population as mean condition increases (Rogers 1987, Noyce and Garshelis 1994). Therefore, survival of juvenile black bears and most aspects of black bear reproduction are influenced to some degree by maternal condition.

Black bear populations in RMNP have remained at low levels (<25) for decades (Baldwin 2008), and demographics of this population are poorly understood. Further, development around RMNP and increasing visitor use (2.6 million visitors versus 3.0 million visitors annually from 1984 to 1991 and 2003 to 2006, respectively; K. Sykes, RMNP information office, personal communication) of the park may impact this black bear population, which already is challenged by extremely high elevation habitats with a short growing season (McCutchen 1993). Because productivity and survival rates of black bears in RMNP are uncertain and likely to change over time, it is unclear whether the population is viable without immigration from adjacent populations. Additionally, increased visitor use and development around RMNP could bring bears into contact with humans, thereby increasing the potential for human–bear conflicts (Madison 2008). Therefore, we assessed the condition, survival, and reproductive parameters of black bears in RMNP to determine the current status of this bear population. Our objectives included: (1) to estimate survival for adult and subadult male and female black bears for the historic and contemporary periods, (2) to estimate reproductive parameters for both the historic (1984–1991) and contemporary (2003–2006) periods and compare to western United States averages, and (3) to compare body condition between historic and contemporary periods to assess their influence on reproductive parameters.

Study area

Rocky Mountain National Park is a 1,080-km^2 park located in the Rocky Mountain Front Range of north-central Colorado. Topography in RMNP consisted of high mountainous peaks interspersed with small subalpine meadows, lakes, streams, glaciers, and tundra at higher elevations. Elevation ranges from 2,400 to 4,345 m. The continental divide bisects RMNP, creating different climatic patterns and vegetation types to the east and west. The eastern park is drier, with precipitation averaging 35 cm in the town of Estes Park. Western RMNP is more mesic, with precipitation averaging 50 cm in the town of Grand Lake. Seventy-five percent of precipitation typically falls during April to September. In Estes Park, mean daily high temperatures range from 7° C in February to 27° C in July, whereas in Grand Lake, mean daily high temperatures range from 0° C in December and January to 23° C in July.

Vegetation community composition varies greatly with elevation and precipitation in RMNP, with more productive communities found on western slopes and at higher elevations (Beidleman et al. 2000). Montane forests and valleys west of the continental divide are comprised primarily of lodgepole pine (*Pinus contorta*) and aspen (*Populus tremuloides*) interspersed with grass- (Poaceae) and sedge- (Cyperaceae) dominated herbaceous meadows. Montane forests on the eastern slope include the same species, although drier sites often are dominated by ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Psuedotsuga menziesii*). Subalpine habitats vary less between western and eastern slopes and are dominated by Engelmann spruce (*Picea englemannii*) and subalpine fir (*Abies bifolia*), with limber pine (*Pinus flexilis*) occasionally present. Elevations above timberline (approximately 3,500 m) are dominated by tundra and bare rock. Below treeline, wetland and riparian areas are dominated by dense stands of spruce-fir and aspen in forested areas (Salas et al. 2005).

Methods

Capture and radiotracking

We captured black bears using modified Aldrich foot snares, culvert traps, and wire-cage traps from 1984 to 1991 (data supplied by L. Zeigenfuss, USGS, and supplemented by McCutchen 1993) and from 2003 to 2006. We also recaptured bears at den sites during the contemporary period. We immobilized black bears with a 5:1 mixture of ketamine hydrochloride and xylazine hydrochloride (200 mg ketamine and 40 mg xylazine/ml). We placed bears into appropriate sex and age categories (subadult versus 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). Additionally, during the historic period (1984–1991), the first premolar was pulled to determine specific age. We collected morphometric data including dorsal contour length (cm; tip of the nose to the base of the tail; Figure 1), straight-line body length (cm; straight line distance from the tip of the nose to the end of the last tail vertebra), girth (cm; circumference of the chest immediately behind the front legs with lungs in deflated position), and weight (measured to the nearest kg using a spring scale). These measurements were recorded during initial captures (June–September, hereafter referred to as summer) and during the early denning period (October–December, hereafter referred to as winter). We radiotracked individuals from May through the time of den entrance. We obtained locations of bears as often as possible, with locations typically recorded a minimum of once per week through a combination of direct observation and triangulation. Occasionally, we also conducted aerial surveys to collect location data from the historic period, as well.

Body condition estimation

For the contemporary period (2003–2006), we used bioelectrical impedance analysis (BIA) during den checks and capture events to estimate percentage of body fat (BF) in females (Farley and Robbins 1994, Hilderbrand et al. 1998). For resistance measurements, we placed bears in a sternally recumbent position with hind legs extended backward and front legs extended forward parallel to the length of the body, with bears placed on a plastic tarp to eliminate conductivity problems associated with ground moisture (Farley and Robbins 1994, Atkinson and Ramsay 1995). We 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). We took measurements multiple times to verify readings.

Additionally, we calculated body condition index scores for female black bears using straight line body length and weight (Cattet et al. 2002). Body condition index (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. Because BF was not measured for the historic period, we used the following regression equation ($F_{2,11} = 141$, $P < 0.001$, $R^2 = 0.962$; Baldwin 2008) to predict BF from BCI scores:

$$BF = 7.070 + (8.915 \times BCI) + (1.823 \times BCI^2)$$

In some situations, weight (6 bears) and straight line body length (10 bears) were not available for individual bears, so we calculated BCI scores from estimated weights and straight line body length for historic and contemporary black bear data (Baldwin 2008). We then used those BCI scores to estimate BF using the modeled relationship. Last, we tested for differences in BCI, BF, and weight between contemporary and historic RMNP black bear data during the summer season using randomization tests (bootstrapping; Efron and Tibshirani 1993, Bender et al. 1996) given that condition data were not normally distributed and because nonparametric bootstrapping is robust for small sample sizes. We ran 1,000 bootstrap iterations with replacement of the difference in mean condition scores between the 2 periods allowing us to compare the distribution of ranked differences. The proportion of values <zero indicated the probability that mean condition values were

Figure 1. Author measuring dorsal contour length for inclusion in body fat estimation.

greater during the historic period as compared to the contemporary bear population.

Survival and cause-specific mortality

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

Table 1. Survival estimates for historic (Hist = 1985–1990) and contemporary (Cont = 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
Hist	$\bar{x}$	1.0	1.0	1.00	0.5	0.9	0.7	0.8
	n	6	5	11	6	7	13	24
	SE	0.0	0.0	0.00	0.1	0.1	0.2	0.1
Cont	$\bar{x}$	0.9	1.0	0.96	0.5	0.9	0.8	0.9
	n	4	4	8	2	4	6	14
	SE	0.1	0.0	0.04	0.0	0.1	0.1	0.1

Cub production

We determined production and survival of cubs from late-winter den checks and from observations of cubs-at-heel (Figure 2). We recorded age of primiparity from known-age bears, and 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 radiocollared bears. We calculated 90% CIs around estimates of natality and recruitment using N = 1,000 bootstrap iterations of the means and SEs of each independent variable (Bender et al. 1996). We compared reproductive parameters between historic and contemporary periods in RMNP, and to other populations throughout the western United States to assess the current and historic status of RMNP's black bear population.

Figure 2. Contemporary cub survival was higher than historic levels in Rocky Mountain National Park likely due to increased maternal condition.

Table 2. Female black bear reproductive parameters for historic (1984–1991) and contemporary (2003–2006) periods in Rocky Mountain National Park, Colorado, as well as mean values for the western United States. All values are means and include age of primiparity, litter interval, litter size, cub survival, natality (cubs/female/year), and recruitment (yearlings/female/year).

	Age of primiparity	Litter interval	Litter size	Cub survival	Natality	Recruitment
RMNP historic	7.5		1.8	0.4		
RMNP contemporary	4.5[a]	2.5	1.8	0.7	0.70	0.5
Western U.S.	5.2[b]	2.6[c]	1.8[d]	0.7[e]	0.7[f]	0.5[f]

[a] Only 1 individual included.
[b] Beck 1991; Beecham 1980; Costello et al. 2001; Frost 1990; Goodrich 1990; Jonkel and Cowan 1971; Kasworm and Their 1994; Tolman 1998; T. Wertz, U.S. Fish and Wildlife Service, Fairbanks, AK, personal communication.
[c] 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, U.S. Fish and Wildlife Service, Fairbanks, Alaska, personal communication.
[d] Beck 1991; Beckmann and Berger 2003; 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, U.S. Fish and Wildlife Service, Fairbanks, Alaska, personal communication.
[f] Natality and recruitment calculated from mean values of interbirth interval, litter size, and cub survival.

Table 3. Comparison between body condition index (BCI), percentage of body fat (BF), and weight (kg) of female black bears during summer in Rocky Mountain National Park, Colorado, for historic (1984–1991) and contemporary (2003–2006) sampling periods.

	BCI			BF			Weight		
Period	$\bar{x}$[a]	SE	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE	*n*
Historic	0.7A	0.2	10	15A	2.4	10	51.8A	5.0	10
Contemporary	1.4B	0.4	7	24B	5.3	7	59.2B	5.3	8

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

Results

Life history information was available for 24 radiocollared black bears (6 adult males, 5 adult females, 6 subadult males, and 7 subadult females) from 1985 to 1990 and 14 radiocollared black bears (4 adult males, 4 adult females, 2 subadult males, and 4 subadult females) from 2003 to 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, with harvest-specific mortality rates of 0.33 in 1985, 0.11 in 1987, 0.16 in 2004, 0.12 in 2005, and 0.00 in all other years for a mean of 0.07 over all years (1985–1990 = 0.07, 2003–2006 = 0.07). All other causes of mortality were unknown.

During the historic period, we observed 9 litters totaling 16 cubs (8 male, 8 female; $\bar{x}$ = 1.8 cubs/litter, SE = 0.15; Table 2). Interbirth interval was not available for historic births. Age of primiparity was documented for 2 females during the historic period ($\bar{x}$ = 7.5 years, SE = 0.5). Cub survival was 0.4, as per McCutchen (1993); *n* and SE were not provided. Because of the absence of interbirth interval data historically, natality and recruitment could not be calculated.

During the contemporary period, we observed 7 cubs through 4 birthing events by collared black bears ($\bar{x}$ = 1.7 cubs/litter, SE = 0.2); we counted 4 cubs in the den, while we observed three at heel. Of the four we observed in dens, two were male and two were female.

The sex of the other cubs was unknown. Interbirth interval for 2 females was 2.5 years (SE = 0.5). We recorded age of primiparity for 1 bear (4 years). One additional female had not reproduced by age 5 when the study ended and was not likely to reproduce at age 6 in winter 2007 (BF = 22%). Cub survival was 0.71 (SE = 0.1). We estimated natality at 0.70 (90% CI = 0.48–1.08) cubs/female/year; recruitment averaged 0.5 (90% CI = 0.26–0.76) yearlings/female/year. All reproductive values observed from the contemporary period were similar to mean values reported throughout the western United States (age of primiparity = 5.2, SE = 0.1; interbirth interval = 2.6, SE = 0.14; litter size = 1.76, SE = 0.05; cub survival = 0.72, SE = 0.08; natality = 0.68, 90% CI = 0.62–0.76; recruitment = 0.49, 90% CI = 0.39–0.59; Table 2).

We observed increased condition of females during the contemporary period, as BCI (historic $\bar{x}$ = 0.72 [SE = 0.2], contemporary $\bar{x}$ = 1.42 [SE = 0.3]; P = 0.02), BF (historic $\bar{x}$ = 15.0% [SE = 2.4], contemporary = 24.4% [SE = 5.3]; P = 0.01), and weights (historic $\bar{x}$ = 51.8 kg [SE = 5.0], contemporary $\bar{x}$ = 59.2 kg [SE = 5.3]; P = 0.09) of females were all higher during the contemporary period than those observed historically (Table 3).

Discussion

Black bear reproduction and cub survival are closely related to the condition of maternal females (Rogers 1987, Elowe and Dodge 1989, Noyce and Garshelis 1994, Beckmann and Berger 2003, Costello et al. 2003). Therefore, an increase in condition of female black bears such as we observed in RMNP (Table 3) should result in greater reproductive success of females, particularly for the survival of juveniles and the 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 is a primary factor regulating black bear populations (Powell et al. 1996). The historic cub survival rate in RMNP was among the lowest recorded for black bears (Garshelis 1994), although contemporary levels were similar to those of other populations throughout the western United States (Table 2). 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 it is usually observed only with females in very poor condition (Minnesota = 65 kg; Noyce and Garshelis 1994). The historically low weights ($\bar{x}$ = 60 kg) and poorer condition of female black bears suggest that these bears often may have 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 lightweight females are more likely to produce lightweight yearlings (Garshelis 1994, Noyce and Garshelis 1994). Further, weights close to 10 kg can predispose yearlings to increased mortality (Noyce and Garshelis 1994), and yearling survival (0.70; L. Zeigenfuss, USGS, unpublished report, 2001) was low for black bears in RMNP during the historic period, compared to those in adjacent populations (i.e., west-central Colorado = 0.94; Beck 1991). Thus, increased nutritional condition of black bears in RMNP (Table 3) likely resulted in increased bear productivity observed contemporarily, regardless of whether increases were due to incremental increases in black bear condition or through exceeding critical thresholds.

Most causes of cub mortality were unknown during this study, although malnutrition and infanticide were observed during the historical period (McCutchen 1993). While the 2 known cubs that died during the contemporary period appeared healthy, their mother was in poorer condition (summer BF = 14%) than other females in RMNP, so we 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 (e.g., predation, infanticide, etc.; Gaillard et al. 2000). Because infanticide and predation are 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 observed in the contemporary period.

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 our 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 (winter: BCI = 1.9, BF = 34%, weight = 94 kg), as age of first reproduction is influenced by body size and presumably absolute condition (Beecham 1980, Rogers 1987, Beck 1991, Samson and Huot 1995). Later reproduction (≥6 years old) was noted for the other nulliparous female observed contemporarily. However, this female resided almost exclusively in wildland areas and was consistently in poorer condition (winter: BCI = 1.3, BF = 22%, weight = 67 kg), whereas the earlier reproducing female was frequently located in heavy human-use areas. This proximity to human-use areas likely resulted in greater consumption of anthropogenic foods by the earlier reproducing female (Baldwin 2008), thus increasing habitat potential of the landscape to levels greater than those associated solely with natural foods. Black bear condition in RMNP was positively related to use of human-use areas during autumn (the season most closely tied to fat accretion in black bears; Baldwin 2008), and consumption of anthropogenic foods by bears in RMNP increased 15 times between the 2 study periods (Baldwin 2008). The later reproducing female likely 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 ≥6 years, respectively). Further, black bears were reported to avoid human-use areas historically (McCutchen 1990). This avoidance likely precluded the use of most anthropogenic foods, thereby reducing the reproductive output of historic bears. Therefore, increased nutrition for nulliparous females from greater use of human-derived foods likely reduced the age of primiparity for some black bears in RMNP and could lead to greater cub production in the future. A similar scenario was observed in Nevada (Beckmann and Berger 2003, Beckmann and Lackey 2008) and further supports the sensitivity of reproduction to nutritional condition.

We saw no changes in litter size between contemporary and historic data in RMNP, and litter sizes were similar to others from Colorado and the West (Table 2). Litter size appears to be less sensitive to maternal condition, although conclusions vary by study (McDonald and Fuller 2001), and 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), so litter size may increase only near the peak of condition. While maximum condition levels for black bears are unknown, contemporary females in RMNP showed levels of condition (BF = 24%; BCI = 1.4; weight = 59.2) that were higher than historic levels (BF = 15%; BCI = 0.7; weight = 51.8) without an increase in litter size. Thus, it is possible that it is absolute size and condition that influences litter size more than relative condition, particularly given that most previous work used weight to index condition. We were unable to assess changes in interbirth interval as such data were unavailable from the historic period. In the contemporary period, black bears in RMNP exhibited intervals comparable to other populations in the western United States (Table 2). 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 cub production between sample periods in RMNP.

Despite low cub survival and later ages of primiparity, 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 is 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 black bears (Freedman et al. 2003) due to its influence on cubs and cub survival (Bunnell and Tait 1981, 1985; 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 may have been too low to maintain the black bear population in RMNP historically without significant immigration.

Unfortunately, we were not able to eliminate variability in natural food sources as a possible explanation for the differences in bear demographics between the 2 study periods, as these data were not collected. Nonetheless, we do not believe food production was substantially different between these study periods, given that RMNP's vegetation has not been altered in the last 20 years and that precipitation amounts did not differ between the study periods (April–September, $\bar{x}$ precipitation [cm]: historic = 31.0 [SE = 4.4], contemporary = 27.2 [SE = 3.7]; $t = 0.55$, $P = 0.60$; J. Visty, RMNP research administrator, personal communication). Alternatively, although black bears in RMNP historically exhibited cryptic behavior and avoided heavy human-use areas (McCutchen 1990), continued development along the boundary of RMNP and increased visitor use (K. Sykes, RMNP Information Office) has increased the potential for human–bear encounters (L. Zeigenfuss, USGS, unpublished report, 2001). For example, black bears in the contemporary population used human-use areas at a greater rate than that observed historically (70% versus 51% of bear locations found in human-use areas [Baldwin 2008). Additionally, denning sites selected closer to trails contemporarily [746 m versus 1,127 m; $P < 0.10$], Baldwin and Bender 2008) resulted in higher cub survival and younger age of primiparity for bears using anthropogenic foods due to increased nutritional condition they provided.

Although increased productivity initially appears positive for bears, as it can facilitate population persistence, it may be offset by increased mortality due to the destruction of problem individuals resulting from negative human–bear encounters (Beckmann and Lackey 2008). We noted 1 such encounter during this study. The first human attack by a black bear in RMNP since 1971 occurred in 2003, with this bear subsequently being euthanized. Additionally, following the conclusion of this study, a formerly radiocollared bear was euthanized for repeated damage to property. This bear was the same individual that reproduced at 4 years of age, further indicating that although supplementation of bear diets with anthropogenic foods may increase reproductive output, it may also result in lower survival, thereby reducing or eliminating the positive effects of food supplementation on overall population productivity (Thiemann et al. 2008, Ziegltrum 2008).

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 (Baldwin 2008). Increased use of human-associated areas and foods, however, has the potential to decouple the RMNP black bear population from such natural climatic limitations, thereby increasing both the reproductive output of bears in RMNP and the potential for human–bear conflicts through higher population growth potential. Improvements of natural foods and habitats, such as those derived from prescribed let-burn, wildfire management or other habitat manipulations, could provide a sustainable strategy for increasing black bear productivity while minimizing bear–human conflicts.

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