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NUTRITIONAL CONDITION OF ELK IN ROCKY MOUNTAIN NATIONAL PARK

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ABSTRACT.—We tested the hypothesis that elk in Rocky Mountain National Park (RMNP) were at ecological carrying capacity by determining herd-specific levels of nutritional condition and fecundity. Ingesta-free body fat levels in adult cows that were lactating were 10.6% (s = 1.7; range = 6.2–15.4) and 7.7% (s = 0.5; range = 5.9–10.1) in November 2001 for the Horseshoe and Moraine Park herds, respectively. Cows that were not lactating were able to accrue significantly more body fat: 14.0% (s = 1.1; range = 7.7–19.3) and 11.5% (s = 0.8; range = 8.6–15.1) for the Horseshoe and Moraine Park herds, respectively. Cow elk lost most of their body fat over winter (April 2002 levels were 3.9% [s = 0.4] and 2.9% [s = 0.4] for the Horseshoe and Moraine Park herds, respectively). Nutritional condition indicated that both Horseshoe Park and Moraine Park elk were well below condition levels elk can achieve on very good–excellent nutrition (i.e., >15% body fat; Cook et al. 2004) and were comparable to other free-ranging elk populations. However, condition levels were higher than those expected at a "food-limited" carrying capacity, and a proportion of elk in each herd were able to achieve condition levels indicative of very good–excellent nutrition. Elk in RMNP are likely regulated and/or limited by a complex combination of density-independent (including significant heterogeneity in forage conditions across RMNP's landscape) and density-dependent processes, as condition levels contradict a simple density-dependent model of a population at ecological carrying capacity.

Key words: Cervus elaphus, *condition, ecological carrying capacity, elk, nutrition.*

Elk (*Cervus elaphus*) in Rocky Mountain National Park (RMNP) were hypothesized to be at ecological carrying capacity (ECC; Lubow et al. 2002), i.e., a "food-limited" carrying capacity where decreased per capita forage acquisition has resulted in decreased individual and population productivity and increased mortality, so that populations are recruiting only enough new individuals to balance annual mortality (Caughley 1979). Elk and other large herbivores respond to increasing density via intrinsic regulatory mechanisms (i.e., density dependence), including decreases in individual condition, juvenile fecundity, juvenile survival, adult fecundity, and lastly adult survival, that are ultimately expressed in population rate-of-increase (Gaillard et al. 2000). Fundamentally, habitat conditions affect elk populations by influencing energy balance and, ultimately, fat reserves of individual elk (Mautz 1978, Franzmann 1985, Cook et al. 2004). In turn, condition of individuals strongly influences virtually every health, production, and survival parameter of elk and other ungulates (Clutton-Brock et al. 1982, Verme and Ullrey 1984, Adams et al. 1995, Keech et al. 2000, Cook 2002, Cook et al. 2004). Nutritional condition of individuals thus provides a direct collation of habitat quality because effects of density-driven resource limitations first involve reductions in nutrition and subsequently condition (Mautz 1978, Franzmann 1985). However, large herbivores can also show poor condition independent of density effects if nutrition is limiting through density-independent mechanisms; for example, if forage quality is inadequate regardless of elk density (Cook et al. 2004).

Nutritional condition can also be related directly to adequacy of elk diets to support key life processes. Levels of condition have been identified that influence basic life-history parameters in elk (Cook et al. 2004); for example, cow elk essentially cease to ovulate and thus do not breed when total body fat levels in autumn drop below 6%. Moreover, dietary quality necessary to achieve specific levels of condition in elk has been identified in studies with penned elk (Cook et al. 2004).

The most common cause of dietary deficiencies is thought to be resource limitations due to competition at high elk densities because of negative feedback in per capita resource capture

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associated with increased population densities or shifts in plant species composition brought about by excessive herbivory (e.g., density effects; Irwin et al. 1994, Riggs et al. 2000). Elk populations experiencing resource limitations from density effects show lower condition than populations not experiencing density effects (Clutton-Brock et al. 1982, Cook 2002) because the former suffer restricted nutrition. To test the hypothesis that elk in RMNP were at ECC, we therefore determined nutritional condition (ingesta-free body fat) of elk as a collation of habitat quality and related condition to the adequacy of the elk nutritional environment. Further, we determined fecundity of adult elk. We hypothesized that if elk in RMNP were at ECC, they should exhibit low condition consistent with diets of very low quality and decreased fecundity. Moreover, survival of adult elk would be affected if a population were at ECC (Gaillard et al. 2000).

STUDY AREA

Rocky Mountain National Park is a 108-km^2 biosphere reserve located in the Rocky Mountain Front Range of north central Colorado. Topography in RMNP was shaped by glaciation and consists of high mountainous peaks interspersed with small subalpine meadows (parks), lakes, streams, glaciers, and alpine tundra at higher elevations. Elevations range from 2440 m to 4345 m at Longs Peak. The Continental Divide bisects RMNP, creating differing climatic patterns to the east and west. Eastern RMNP is drier, with annual precipitation averaging 35.1 cm at Estes Park. Western RMNP is more mesic, with precipitation averaging 50.8 cm at Grand Lake. Seventy-five percent of the precipitation falls from April to September. Mean daily high temperatures range from 3.6°C in January to 25.7°C in July at Estes Park.

Vegetation at RMNP includes more than 700 species of plants. Lower slopes and valleys are composed of forests of lodgepole (*Pinus contorta*) and ponderosa pine (*P. ponderosa*), blue spruce (*Picea pungens*), Douglas-fir (*Pseudotsuga 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. engelmannii*) and subalpine fir (*Abies lasiocarpa*) predominate. Elevations above timberline are dominated by alpine tundra and bare rock.

Wildlife in RMNP includes a diverse fauna dominated by large mammals, i.e., elk, Rocky Mountain bighorn sheep (*Ovis canadensis*), mule deer (*Odocoileus hemionus*), moose (*Alces alces*), black bear (*Ursus americanus*), mountain lion (*Felis concolor*), lynx (*Lynx canadensis*), and coyote (*Canis latrans*).

Elk wintering in eastern RMNP are split between 2 wintering populations: the Horseshoe Park and Moraine Park herds (Lubow et al. 2002). Elk densities in Moraine Park average approximately 3 times higher than in Horseshoe Park; peak densities in certain portions of the winter range can exceed 90 elk · km^{-2} (Singer et al. 2002). Vegetation impacts are also greater in Moraine Park than in Horseshoe Park (Singer et al. 2002). Despite these differences, the herds are often treated as a single population for modeling, and discussions of elk-ECC in RMNP consider the elk as a single population (Lubow et al. 2002, Singer et al. 2002). Overall, elk densities were >30 elk · km^{-2} on 7% of RMNP's winter ranges, and <1–29 elk · km^{-2} on the remaining 93% (Singer et al. 2002). Bull:cow ratios averaged 22 bulls per 100 cows in RMNP (Lubow et al. 2002).

Our data represent a one-time look at elk condition and, consequently, nutrition in RMNP. Generality of our results is dependent upon generality of spring, summer, autumn, and winter conditions experienced by elk from April 2001 to April 2002. Comparisons of monthly mean temperature and total precipitation deviations with long-term means for Estes Park indicated that neither summer–autumn conditions (mean temperature deviation = +1.04°C [95% CI = –0.23–1.69]; mean precipitation deviation = –0.20 cm [95% CI = –2.31–1.96]) nor winter (mean temperature deviation = –2.52°C [95% CI = –5.26–0.23]; mean precipitation deviation = +0.61 cm [95% CI = –0.56–1.78]) conditions differed from long-term averages (National Climate Data Center archived data). Thus, our data should be indicative of mean conditions for elk in RMNP.

MATERIALS AND METHODS

Elk Capture

We captured 59 cow elk >1.5 years of age (range = 2.5–12.5), 14 from the Moraine Park

Table 1. Total percent ingesta-free body fat (s) of cow elk from the Horseshoe Park and Moraine Park herds, Rocky Mountain National Park, November 2001 and April 2002.

	Horseshoe Park		Moraine Park	
Class	November	April	November	April
Nonlactating	14.0 (1.1)A[1]		11.5 (0.8)B	
Lactating	10.6 (1.7)B		7.7 (0.5)C	
All		3.9 (0.4)D		2.9 (0.4)D

[1]Means sharing a letter do not differ ($P > 0.05$).

and 15 from the Horseshoe Park herds in November 2001, and 15 from each herd in April 2002. We captured elk by ground-darting using carfentanil citrate and xylazine hydrochloride (1.5 mg carfentanil citrate + 300 mg xylazine per elk). Immobilized elk were given antibiotics, vitamin E/selenium, vitamin B, and an 8-way *Clostridium* bactrain. Following processing, the immobilants were reversed with 150 mg of naltrexone + 1000 mg of tolazoline per elk. Elk were aged using tooth eruption and wear (Quimby and Gaab 1957) and were temporarily marked with an oil-base paint to avoid recapture of the same individuals.

Nutritional Condition and Fecundity

We estimated ingesta-free body fat of elk at each capture using a live animal index, which combined subcutaneous fat depth at the rump measured by a large-animal ultrasound with a body condition score (rLIVINDEX; Cook et al. 2001). When ultrasonography was not possible, we used a body condition score (rBCS; Cook et al. 2001). The rBCS involved classifying fat and muscle catabolism along the sacral ridge, ilium, ishium, and sacro-sciatic ligament into condition classes (Cook 2000). Both methods are strong predictors ($r^2 = 0.86–0.90$) of total ingesta-free body fat in elk (Cook et al. 2001).

We used 2-way ANOVA (Zar 1996) to compare fat levels among classes of cows (lactating, nonlactating) and seasons (November, April), and Student's 2-tailed t test (Zar 1996) to compare body fat between Horseshoe Park and Moraine Park elk in November for both lactation classes pooled. We assessed pregnancy in November using ultrasonography and in April by rectal palpation and blood progesterone (Weber et al. 1982, Bingham et al. 1990). We determined lactation status of each captured cow in November by presence/absence of milk in the udder (Bender et al. 2002). We computed variances around proportions pregnant and proportions lactating using the normal approximation (Zar 1996) and compared proportions pregnant in November and April for each herd using Fischer's exact test (Zar 1996).

RESULTS

Nutritional Condition and Fecundity

Ingesta-free body fat differed between sites and by lactation status ($F_{5,53} = 46.80$; $P < 0.001$). In November elk had more body fat than in April for either site (Table 1). Elk that were lactating in November had less fat than cows that were not lactating in either herd. Both lactating and nonlactating cows in Horseshoe Park had greater fat levels than in Moraine Park in November (Table 1). Population-level (lactating and nonlactating elk combined) body fat levels in November were also higher for Horseshoe Park ($\bar{x} = 12.8\%$, $s_{\bar{x}} = 0.98$, range = 6.2–19.3) than Moraine Park ($\bar{x} = 9.7\%$, $s_{\bar{x}} = 0.68$, range = 5.9–15.1; $s_{\bar{x}} = 2.59$, $P = 0.015$). Fat levels of cows did not differ between herds in April (Table 1).

Proportion of pregnant females did not differ between females captured in November and April in either Horseshoe Park (Fischer's exact test $P = 0.402$) or Moraine Park (Fischer's exact test $P = 0.275$). Proportions were pooled for overall rates of 0.86 ($s_{\bar{x}} = 0.06$; 25/29) and 0.63 ($s_{\bar{x}} = 0.09$; 19/30) for Horseshoe and Moraine Parks, respectively.

DISCUSSION

Lactating cow elk in RMNP exhibited condition levels indicative of either marginal (Horseshoe Park) or poor (Moraine Park) quality summer–autumn diets (Cook et al. 2004).

Body fat in late autumn averaged 7.7% in Moraine Park and 10.6% in Horseshoe Park. Marginal diet quality (2.40–2.75 kcal of digestible energy per gram of forage [kcal · g^{-1} DE], allowing accretion of 8%–12% body fat) may influence reproduction and survival through enhanced probability of winter mortality, delayed breeding, reduced fecundity, and delayed puberty. Poor diet quality (dietary qualities of <2.40 kcal · g^{-1} DE, allowing accretion of <8% body fat) can markedly affect reproduction and reduce survival probabilities (Cook et al. 2004). Thus, conditions indicated that nutritional deficiencies should exert a moderate (Horseshoe Park) to strong (Moraine Park) limiting effect on elk productivity in RMNP, primarily through reduced pregnancy rates, delayed puberty, some increase in overwinter mortality depending upon weather severity, and delayed breeding (Cook et al. 2004), particularly in the Moraine Park herd. Fecundity data from both populations (Horseshoe Park = 86% pregnancy; Moraine Park = 63% pregnancy) supported these assertions. Differences in fat levels between elk from Horseshoe and Moraine Parks likely reflect differences in quality of elk summer ranges (see below) and elk densities, which were approximately 3 times higher in Moraine Park; ≤90 elk · km^{-2} compared to ≤29 elk · km^{-2} (Singer et al. 2002).

Fat levels of elk in RMNP also showed that a proportion of cows in both herds were able to achieve very good–excellent condition (5/14 and 1/15 cows achieved body fat levels >15% in November for Horseshoe and Moraine Park herds, respectively). Fat levels in late November reached as high as 19.3% for nonlactating cows in Horseshoe Park, the highest fat level yet recorded for free-ranging elk (Cook et al. 2002), and a lactating elk reached 15.4% in Horseshoe Park. In Moraine Park, nonlactators (maximum = 15.1%) and lactators (maximum = 10.1%) were unable to reach levels observed in Horseshoe. The higher levels (15%+) were indicative of very good to excellent nutrition (≥2.85 kcal · g^{-1} DE; Cook et al. 2004). Moreover, the variation in fat levels of elk in RMNP in autumn was also the highest yet recorded for free-ranging elk (Cook et al. 2002). This was true even within lactation status categories; fat levels of lactating cows ranged from 5.9% to 15.4%. Because fat levels of lactating cows in autumn are strongly related to forage quality consumed in summer and early autumn (Cook et al. 2004), these data indicate that summer forage conditions used by elk in RMNP varied markedly. While differences in density between elk in Horseshoe and Moraine Parks may explain some of the range in fat levels for nonmigratory individuals, it is likely that variations in microclimate, topography, and soils across RMNP's landscape (Arthur and Fahey 1993, Hessl et al. 1996, Kalkhan and Stohlgren 2000) also influenced elk condition. That is, some elk probably occupied areas of unusually high forage quality and quantity (e.g., high-elevation riparian meadows), while other elk occupied summering areas supporting poor forage conditions (e.g., remaining in Moraine or Horseshoe Parks throughout the year). This suggests an important density-independent influence on elk productivity, driven by differential range use and thus exposure to forage differing substantially in quality. Further, because diet quality needs to be maintained throughout the summer–autumn period to achieve these high levels of condition, an elk range near ECC would be unable to provide this level of dietary quality due to deterioration of range conditions associated with overutilization (Irwin et al. 1994, Riggs et al. 2000).

Adult survival is the last demographic affected by resource limitations, but it should decline when a population faces severe resource limitations as when at ECC (Gaillard et al. 2000). Lubow et al. (2002) documented an adult cow survival rate of 0.93 in RMNP, the 2nd highest survival rate published for adult cows, behind only the 0.97 documented by Ballard et al. (2000) for unhunted elk in Arizona. Thus, adult survival appears unaffected by density in RMNP, further indicating that while certainly resource stressed, elk are likely below ECC in RMNP.

MANAGEMENT IMPLICATIONS

Past discussions of ECC for elk in RMNP addressed winter ranges and minimized the influences of summer–autumn range conditions (Hobbs et al. 1982, Lubow et al. 2002). However, the literature clearly shows that summer range conditions have considerable influences on pregnancy rates, calf growth, age at puberty, fat accretion of cows, and ability of elk to survive over winter, as a function of body fat in adults and body size of calves (Clutton-Brock et al. 1982, Cook 2002, Cook et al. 2004). Ecologically, it can be argued that winter ranges are simply a place to stay where harsh winter conditions are minimized and thus rate of condition loss is minimized (Mautz 1978). A definition of carrying capacity for these conditions is ambiguous, because a good winter range is one that reduces the rate of condition loss, while a poor winter range has a relatively higher rate of condition loss. In both situations, elk cannot maintain condition, and thus any estimate of "carrying capacity" would be negative. From a practical perspective, the "carrying capacity" of winter range, or the number of elk that can survive winter on a given piece of ground, is a function of winter forage, winter weather, late-autumn fat levels of adults, and calf size (Mautz 1978, Clutton-Brock et al. 1982, Cook 2002). Winter range "carrying capacity" is thus higher if adult cows are fat and consequently calves are large at the beginning of winter (Mautz 1978). Condition data from RMNP show that both Horseshoe Park and Moraine Park herds lose most of their accumulated fat over winter, although post-winter fat levels remain above levels associated with starvation mortality (~2% body fat; Cook et al. 2004), a pattern in fat catabolism similar to other elk herds for which seasonal condition data are available (Cook et al. 2002). This fat catabolism reflects forage-quality data (Hobbs et al. 1982) that indicate elk in RMNP would be unable to meet maintenance requirements on winter ranges regardless of population densities. Thus, the importance of body fat accretion while on summer range is an undeniably important aspect of the nutritional and population ecology of elk in RMNP. Limiting evaluations to winter range relations, as has traditionally been done, limits insight into elk-habitat relations and elk population status in RMNP.

Condition data also indicate that elk from the Horseshoe Park and Moraine Park herds experienced very dissimilar foraging habitats and that significant variation existed within each herd in terms of the quality of foraging habitats that individuals exploited. A proportion of elk from both herds acquired good–excellent nutrition and thus exploited habitats well above forage-quality and -quantity levels associated with any definition of a range at ECC. Recent assessments of elk-habitat relations in RMNP treated the Horseshoe Park and Moraine Park herds as a single entity (Lubow et al. 2002). Condition data, however, demonstrated that these herds used foraging habitats of significantly differing quality, and thus they should be treated as distinct populations when assessing demographics, given the fundamental influence of nutrition on elk survival and productivity (Clutton-Brock et al. 1982, Cook 2002).

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