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NUTRITIONAL CONDITION OF NORTHERN YELLOWSTONE ELK

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We estimated nutritional condition for 96 female northern Yellowstone elk (*Cervus elaphus nelsoni*) during mid- to late winter 2000, 2001, and 2002. Neither year nor capture location significantly influenced any measure of condition (body fat, body mass, and longissimus dorsi thickness; $P \geq 0.14$). Overall, age = 8.9 years \pm 0.4 SE, body fat = 9.5% \pm 0.4, body mass = 235.1 kg \pm 2.2, and longissimus dorsi muscle thickness = 5.6 cm \pm 0.1. Despite an age segregation pattern across the winter range ($P = 0.016$), we found no evidence of bias in our estimates of nutritional condition due to this pattern because condition was unrelated to age. Yearly pregnancy and lactation rates of all cows ranged from 78 to 84% and 8 to 16%, respectively, at the time of capture. Lactational status significantly influenced body condition ($P = 0.003$), with lactating cows having 50% less body fat than nonlactating cows. Probability of pregnancy observed for elk that we captured followed a logistic curve as a function of body fat levels. Based on mid- to late winter body fat levels, we would predict low mortality of adult cows during mild to normal winters. We suggest the possibility of nutritional limitations acting on this herd through summer–autumn forage conditions, in association with limitations during harsh winters.

Key words: age structure, body fat, *Cervus elaphus*, condition, elk, lactation, reproduction, Yellowstone

Understanding nutritional condition (sensu Harder and Kirkpatrick 1994) can provide important insights into the influence of habitat on population dynamics of free-ranging large ungulates. Probability of breeding in autumn (Cook 2002; Cook et al. 2004; Kohlmann 1999), overwinter survival (Cook et al. 2004; Hobbs 1989), lactation yields of mothers (Loudon et al. 1983; Oftedal 1985), susceptibility to predation (Bender et al. 2002; Mech et al. 2001), and possibly other effects that influence survival and reproduction (Cook 2002) are related to nutrition and nutritional condition. Levels of ingesta-free body fat, a key indicator of nutritional condition (Harder and Kirkpatrick 1994), reflect cumulative energy balance over relatively long periods and provide insights that might be more useful for some applications than those derived from indicators of relatively short-term nutritional status (e.g., urinary chemistry—Cook 2002; DelGiudice et al. 2001).

To our knowledge, body fat of free-ranging cow elk (*Cervus elaphus*) has never been reported, and nutritional condition

determined from fat samples (e.g., femurs, kidneys) collected from elk dying of starvation or killed by hunters has rarely been published. Kohlmann (1999), Stussy (1993), and Trainer (1971) reported kidney fat of hunter-killed cow elk in Oregon; Flook (1970) reported kidney fat indices for elk in Canada; and Greer (1968), Houston (1978), and Mech et al. (2001) reported femur fat levels in Yellowstone elk. Lack of suitable techniques have undoubtedly hampered obtaining estimates of body fat from free-ranging live animals. Recent development of ultrasonography (Cook et al. 2001a, 2001b; Stephenson et al. 1998) and body condition scoring (Cook et al. 2001a, 2001b; Gerhardt et al. 1996) provide new approaches for live animals that are accurate and practical. These techniques have potential to greatly advance understanding of factors that influence nutrition and ways in which nutrition, in turn, affects population dynamics.

We estimated nutritional condition with ultrasonography and body condition scoring of cow elk captured from the northern herd of Yellowstone National Park (YNP) during winters 2000, 2001, and 2002 in association with another study. Here, we present data on nutritional condition, provide an analysis of some of the factors (e.g., lactational status, age) that might account for observed variation in condition levels, and discuss the extent to which nutrition might influence reproduction and survival in this herd.

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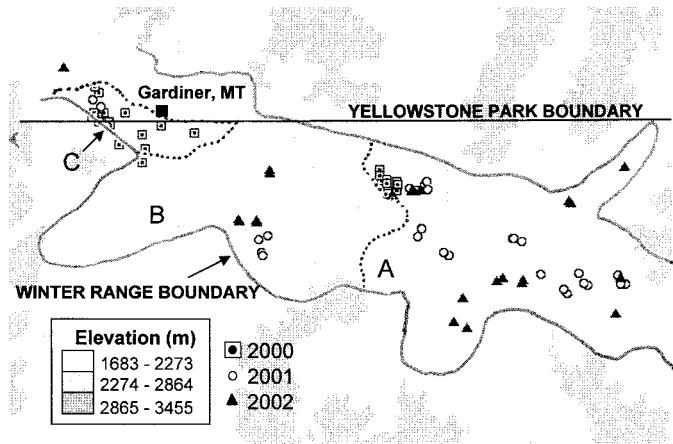


FIG. 1.—Locations of cow elk captured during 2000–2002 in the northern winter range of Yellowstone National Park, illustrating park boundary, A) upper winter range, B) lower winter range, and C) boundary area by Gardiner, Montana (Houston 1982). Locations of 16 elk captured in 2000 were excluded because their precise capture locations were not recorded.

MATERIALS AND METHODS

Yellowstone National Park is an 891,000-ha protected area primarily in northwestern Wyoming with a variety of habitats from high alpine to lower elevation sagebrush (*Artemisia*) grasslands (Despain 1990). The climate is characterized by long, cold winters with substantial amounts of snow and short, cool summers (Cook 1993). The index of winter severity for the Lamar Valley (United States Geological Survey Northern Rocky Mountain Science Center) during the winter months immediately preceding each of our elk captures was 0.18, 0.71, and 2.56 for 2000, 2001, and 2002, respectively (0 = average, <0 = harsher than average, and >0 = milder than average with respect to precipitation and temperature). Growing season precipitation for 1999, 2000, and 2001 differed +2.31, –2.69, and –1.29 cm from the 30-year average for Cooke City, Montana (National Climatic Data Center, Asheville, North Carolina).

Prior to the fires of 1988 and prior to wolf reintroduction in 1995, northern Yellowstone elk numbered an estimated 23,240 animals (Coughenour and Singer 1996b). Numbers recently declined, and about 12,000 elk wintered on the northeastern portion of the park during this study (Northern Yellowstone Cooperative Wildlife Working Group, in litt.). The northern winter range is subdivided into the upper and lower winter ranges and the boundary line area near Gardiner, Montana (Houston 1982; Fig. 1). Elevations on the northern range vary from 1,500 to >2,400 m and increase from west to east (DelGiudice et al. 2001). Even in severe winters, elk inhabit both the lower and upper winter range (Houston 1982). In addition, migration during winter to areas outside of the park has increased since winter 1988–1989 (Lemke et al. 1998). General characteristics and ecology of the northern Yellowstone elk herd are described by Houston (1982) and Coughenour and Singer (1996a).

All elk were handled in accordance with an approved animal welfare protocol (Animal Care and Use Committee 1998). Elk were captured via commercial helicopter net-gunning (Hawkins and Powers, Inc., Greybull, Wyoming) during 15–16 March 2000, 6–8 February 2001, and 2–4 February 2002. Major groups of cow elk were located by sight from fixed-wing aircraft prior to capture, and capture crews were directed to those herds in an attempt to acquire a spatially representative sample of the northern range population of cows that

wintered within the park boundaries. In 2000, major groups were found near Mount Everts (44°58'N, 110°39'W), Hellroaring (44°58'N, 110°28'W), and the Tower areas (44°56'N, 110°25'W), but we were unable to capture elk in the Tower group. During 2002, a special attempt was made to capture cows in the same general area in groups not already represented by elk that had been radiocollared in previous years. We sampled elk from 2 to 7 separate areas of the northern range each year. Only females were captured, and attempts were made to avoid capturing elk that, on the basis of size, appeared to be calves and yearlings.

Captured elk were shackled, blindfolded, and handled without drugs. Capture locations (Universal Transverse Mercator) were recorded on a Garmin III handheld GPS unit (Garmin International, Olathe, Kansas), and each cow was fitted with a Telonics VHF radiocollar (Telonics, Mesa, Arizona). Thirty-five ml of blood was drawn by jugular venipuncture and centrifuged within hours at the staging area. Serum was frozen for up to 4 weeks before being analyzed in triplicate for protein B specific for pregnancy via radioimmunoassay (BioTracking, Moscow, Idaho—Noyes et al. 1997). In 2000, the i4 tooth was extracted following lidocaine injection into the gum to minimize pain, and ages were determined to the nearest year by examination of annuli (Matson's Laboratory, Milltown, Montana—Hamlin et al. 2000). During 2001 and 2002, a vestigial upper canine was extracted, and ages were determined to the nearest year by examination of annuli as above.

Our evaluation of nutritional condition was based on 3 variables: ingesta-free body fat (hereafter referred to as body fat), body mass, and thickness of the longissimus dorsi muscle (the latter provides a relative index of protein catabolism—Cook 2000; Cook et al. 2004; Herring et al. 1995). We evaluated body fat on captured cows with a rump body condition score developed for elk (Cook et al. 2001a, 2001b) and subcutaneous rump fat thickness (Cook et al. 2001a, 2001b; Stephenson et al. 1998) measured via a Sonovet ultrasonograph with a 5.0-MHz, 7.0-cm probe (Universal Medical Systems, Bedford Hills, New York). Brightness mode real-time ultrasonography generates gray scale 2-dimensional images that readily distinguish tissue layers (Stephenson et al. 1998).

Body fat (y) was estimated by the equation

$$y = -7.1527 + 7.3231x - 0.9898x^2 + 0.0574x^3,$$

where x is rLIVINDEX, an arithmetic combination of subcutaneous rump fat thickness and the rump body condition score (Cook et al. 2001a, 2001b).

Thickness of the longissimus dorsi muscle was measured between the 12th and 13th ribs near the backbone by ultrasonography (Cook et al. 2001a, 2001b; Herring et al. 1995).

Body mass was calculated from chest girth measurements with the equations developed for chemically immobilized, sternally recumbent cows (Cook et al. 2003). Chest girth circumference was measured by tightly pulling a cloth tape placed around the chest directly behind the front shoulder and elbows and positioned 7–10 cm posterior to the crest of the thoracic vertebrae (withers—Cook et al. 2003). Because chest girth varies between sternally recumbent and laterally recumbent, hobbled elk, we converted our circumference measurements (x) to a sternally recumbent basis (y) with the equation $y = 0.88x + 15.39$ (Cook et al. 2003) prior to calculation of body mass. The girth circumference–body mass equations of Cook et al. (2003) account for pregnancy status and nutritional condition. For pregnant elk ≥ 1 year old, body mass = $2.29x_1 + 1.30x_2 - 133.46$; for nonpregnant elk > 1 year old, body mass = $1.88x_1 + 1.84x_2 - 89.46$; and for nonpregnant yearlings, body mass = $0.74x_1 + 2.50x_2 + 45.48$, where x_1 is girth circumference (cm) and x_2 is body fat (%).

TABLE 1.—Body condition and productivity of cow elk captured during winter (2000–2002) in northern Yellowstone National Park. Means \pm SE, and ranges (in parentheses) are presented for age (determined from teeth annuli), body fat (determined by ultrasonography and a body condition score), body mass (estimated from girth measurements and regression equations of Cook et al. [2003]), and loin muscle thickness (longissimus dorsi, measured by ultrasonography).

Date of capture	<i>n</i>	Index of winter severity	Pregnant (%)	Lactating (%)	Age (years)	Body fat (%)	Body mass (kg)	Loin thickness (cm)
15–16 March 2000	44	0.18	84.1		7.6 \pm 0.6 (1–15)	8.9 \pm 0.5 (1.8–14.3)	230.2 \pm 3.0 (175.3–261.7)	5.5 \pm 0.1 (4.3–6.6)
6–8 February 2001	28	0.71	78.6	8.7	11.2 \pm 0.8 (5–18)	9.8 \pm 0.8 (1.8–16.0)	240.4 \pm 4.4 (198.9–264.5)	5.6 \pm 0.1 (4.3–6.4)
4–5 February 2002	24	2.56	82.6	16.7	8.7 \pm 0.8 (1–15)	10.1 \pm 0.8 (2.9–15.0)	237.6 \pm 4.4 (175.4–274.9)	5.5 \pm 0.1 (4.5–6.5)
Pooled	96		82.0	12.7	8.9 \pm 0.4	9.5 \pm 0.4	235.1 \pm 2.2	5.6 \pm 0.1

Lactational status was determined for all elk during 2001 and 2002 (lactation was not evaluated in 2000). Cows with an udder from which milk could be extracted were classified as lactating (milk indicates either a cow is still nursing a calf or has been nursing a calf in the previous 3–11 days—Fleet and Peaker 1978; Flook 1970; Noble and Hurley 1999). Cows were classified as previously lactating if the udder was swollen but did not contain milk (normally, semiclear or clear fluid could be extracted). Cows were considered nonlactating if the udder was not swollen and fluid could not be extracted.

Previous observations indicated that cows tended to segregate spatially by lactational status from east to west across the winter range (Houston 1982). Because age or pregnancy status can vary with lactational status, we assessed potential bias in our body condition estimates that could have resulted from spatial distribution of our captures. We plotted capture locations on a 30-m elevation map in Arc View 3.2 software (Environmental Systems Research Institute, Inc., Redlands, California) and calculated the distance from the easting of the easternmost capture location to each capture location occurring to the west. This resulting variable, referred to as the distance from the most easterly capture location, ranged from 0 km for the most easterly capture location to about 45 km for the most westerly locations.

We then determined whether different classes of elk (i.e., age, pregnancy) were segregated across the winter range in each year. We could not do this for lactational status because only 6 elk were still lactating at the time of capture. We used 2 analyses of covariance (ANCOVAs; general linear model procedure—SAS Institute Inc. 1988) to test the effects of distance from most easterly capture location and year and their interaction on spatial patterns of age and pregnancy. Then we evaluated the relationship of our 3 measures of nutritional condition with distance from most easterly capture location and year, again by ANCOVA. If there was no statistical evidence of a spatial or year effect on nutritional condition, distance from most easterly capture location and year were dropped from subsequent analyses.

Our next set of analyses identified factors that accounted for variation in nutritional condition. We tested effects of lactation and age on body fat for years 2001 and 2002 by ANCOVA and examined effects of age on lactational status with logistic regression (categorical models procedure—SAS Institute Inc. 1988). We then tested effects of age and body fat on body mass and loin thickness with the use of multiple regressions (general linear model procedure—SAS Institute Inc. 1988). Lactational status was not included in the latter analysis due to small sample size. Finally, we tested the effects of body fat, age, and their interactions on the probability of pregnancy by logistic regression (categorical models procedure—SAS Institute Inc. 1988). Because we had so few lactating cows, lactational status could not be included in the analysis.

RESULTS

Over 3 years, we evaluated condition of 96 cow elk on the northern winter range within the boundaries of YNP (Table 1; Fig. 1). Capture locations of elk differed among years. Precise capture locations were not recorded (via GPS) for 16 elk in 2000, but the 28 elk whose GPS capture locations were recorded were located at the middle to more westerly areas of the winter range. By contrast, during the 2nd and 3rd years, the majority of elk were captured at more easterly areas of the winter range (Fig. 1).

Age differed by distance from most easterly capture location ($F = 6.14$; $d.f. = 1, 79$; $P = 0.016$) and year ($F = 4.17$; $d.f. = 2, 79$; $P = 0.019$) but not by their interaction ($F = 1.55$; $d.f. = 2, 79$; $P = 0.22$). Older cows were relatively more abundant in the upper winter range to the east, whereas younger cows were more common close to park boundaries in the lower portion of the winter range to the west (Fig. 2). Thus, captured cows tended to be younger during the 1st year of the study, probably because most of the captured elk were in the lower winter range. Pregnancy did not differ with respect to distance from most easterly capture location ($\chi^2 = 0.16$, $P = 0.69$), year

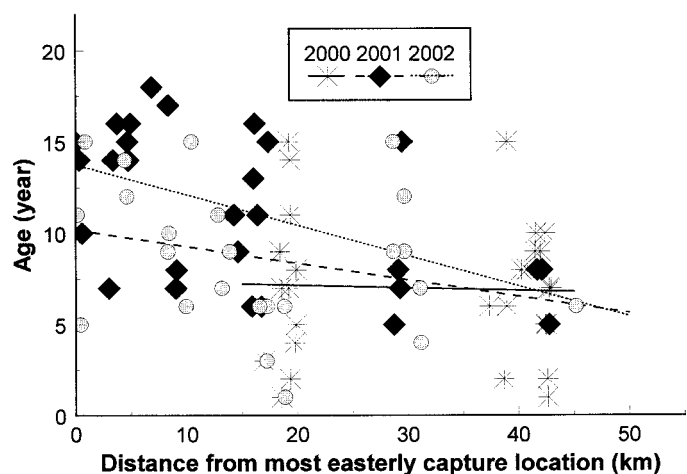


FIG. 2.—Relation of capture location in km (using distance from furthest easterly capture location) to age of elk by year for cow elk captured in northern Yellowstone National Park during winters of 2000–2002.

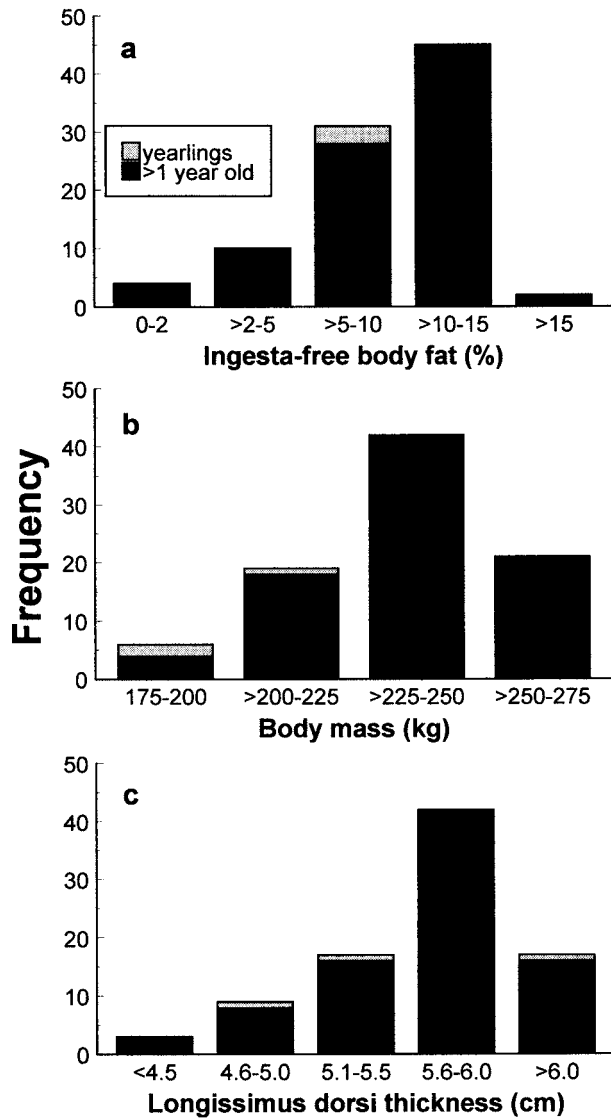


FIG. 3.—Frequency of body condition values: a) ingesta-free body fat (as percentage of total body mass), b) total body mass estimated from girth measurements and regression equations from Cook et al. (2003), and c) thickness of longissimus dorsi muscle for 96 cow elk captured in northern Yellowstone National Park during winters of 2000–2002.

($\chi^2 = 0.16$, $P = 0.69$), or their interaction ($\chi^2 = 0.68$, $P = 0.41$).

Despite differences in age in relation to capture location, we found no significant location effects on our 3 measures of condition among years. Body fat did not differ with respect to distance from most easterly capture location ($F = 0.41$; $df. = 1$, 76 ; $P = 0.52$), year ($F = 0.36$; $df. = 2$, 76 ; $P = 0.70$), or their interaction ($F = 0.17$; $df. = 1$, 76 ; $P = 0.84$). Body mass did not differ with respect to distance from most easterly capture location ($F = 1.36$; $df. = 1$, 73 ; $P = 0.25$), year ($F = 1.94$; $df. = 2$, 73 ; $P = 0.15$), or their interaction ($F = 1.45$; $df. = 1$, 73 ; $P = 0.24$). Thickness of the longissimus dorsi muscle did not differ with respect to distance from most easterly capture location ($F = 2.18$; $df. = 1$, 73 ; $P = 0.14$), year ($F = 1.21$;

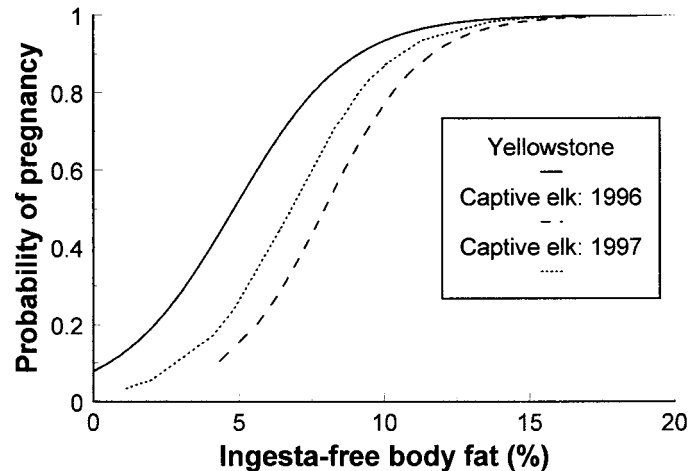


FIG. 4.—Logistic regression of probability of pregnancy (y) on ingesta-free body fat (x) for northern Yellowstone elk during mid-winter 2001–2002 [$y = e^{(2.462-0.511x)} \div (1 + e^{(2.462-0.511x)})$], captive Rocky Mountain elk during the 1996 breeding season, and captive Rocky Mountain elk during the 1997 breeding season (data on captive elk are from Cook et al. [2004] and were based on body fat measured in October each year). Higher pregnancy rates relative to body condition of Yellowstone elk most likely are due to later data collection and the resulting depletion of fat from October to February.

$df. = 2$, 73 ; $P = 0.31$), or their interaction ($F = 0.81$; $df. = 1$, 73 ; $P = 0.45$). Thus for all subsequent analyses of body condition, the variables year and distance from most easterly capture location were eliminated and data were pooled across these variables.

Across years, age = $8.9 \text{ years} \pm 0.4 \text{ SE}$, body fat = $9.5\% \pm 0.4$, body mass = $235.1 \text{ kg} \pm 2.2$, and thickness of the longissimus dorsi muscle = $5.6 \text{ cm} \pm 0.1$. Although the ranges for our condition indices were large (Table 1), the majority (84.8%) of animals had $>5\%$ fat, weighed $>225 \text{ kg}$, and had a longissimus dorsi muscle thickness $>5.5 \text{ cm}$ (Fig. 3). Only a small proportion (4.3%) of animals fell below 2% fat and had a longissimus dorsi muscle thickness $<4.5 \text{ cm}$.

Body fat did not differ with respect to age ($F = 1.08$; $df. = 1$, 86 ; $P = 0.30$) but did differ with respect to lactational status ($F = 6.35$; $df. = 2$, 46 ; $P = 0.003$). Across years, body fat averaged $5.8 \pm 1.8\%$ for lactating cows ($n = 6$), $8.0 \pm 1.7\%$ for previously lactating cows ($n = 9$), and $11.0 \pm 0.6\%$ for nonlactating cows ($n = 32$). Lactational status did not differ with respect to age ($\chi^2 = 0.76$, $P = 0.68$).

Body mass was positively related to body fat ($F = 4.07$; $df. = 1$, 84 ; $P = 0.047$) but did not differ with respect to age ($F = 0.02$; $df. = 1$, 84 ; $P = 0.89$) or their interaction ($F = 1.97$; $df. = 1$, 84 ; $P = 0.16$). We found an age by body fat interaction effect on thickness of the longissimus dorsi muscle ($F = 6.83$; $df. = 1$, 85 ; $P = 0.011$); older cows were thinner than younger cows at low levels of nutritional condition ($<8\%$ body fat).

Probability of pregnancy differed by body fat ($\chi^2 = 18.26$, $P < 0.001$) but did not differ with respect to age ($\chi^2 = 1.97$, $P = 0.16$) or their interaction ($\chi^2 = 0.96$, $P = 0.33$; Fig. 4). Across year and age classes, pregnancy rate averaged 82%

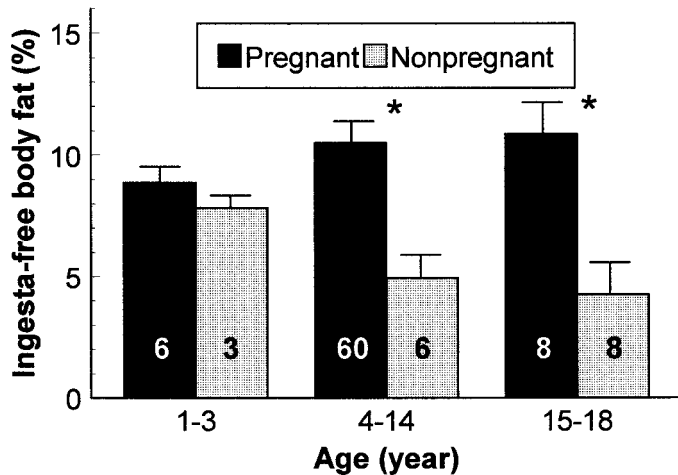


FIG. 5.—Ingesta-free body fat content of young (≤ 3 years old), prime (4–14 years), and old (≥ 15 years) cow elk captured in northern Yellowstone National Park by pregnancy status and age class, shown as mean + SE. Sample sizes are given for each classification; significant differences ($P \leq 0.05$) within age classes are denoted with asterisks.

($n = 94$), and pregnant cows had more fat than nonpregnant cows ($F = 42.30$; $d.f. = 1, 88$; $P < 0.001$; Fig 5). We grouped elk into 3 age categories on the basis of pregnancy rates (Fig. 5): young (1–3 years), prime (4–14 years), and old (15+ years). Although sample sizes were small for ages 12–14 years and declines might have occurred during these ages, pregnancy rates declined markedly after age 14 years (Fig. 6). Pregnancy rates were 67% for young cows ($n = 10$, including 3 yearlings; 2 nonpregnant), 91% for prime cows ($n = 66$), and 50% for old cows ($n = 16$).

DISCUSSION

Since implementation of the natural regulation policy for ungulates in YNP in 1969 (Houston 1982), there has been much interest in density-dependent population regulation, particularly the interactions of food limitations on winter range with elk numbers, population growth, and productivity (e.g., Coughenour and Singer 1996a; Houston 1982; Taper and Gogan 2002). Our estimates of nutritional condition are relevant to this discussion because nutritional condition, particularly when indexed by body fat, reflects adequacy of forage quality and quantity (Cook et al. 2004; Parker et al. 1999) and can strongly influence reproduction and survival (Cook 2002; Cook et al. 2004; Harder and Kirkpatrick 1994; Kohlmann 1999; Trainer 1971; Verme and Ullrey 1984).

Body fat of cow elk varies from about 1% to $>20\%$, (Cook et al. 2004), and body mass of adult Rocky Mountain cow elk ranges from 180 to 320 kg (Cook et al. 2004; Hudson et al. 1991). Body fat levels (1–16%) and body mass (189–275 kg) of Yellowstone cow elk spanned much of these ranges during February and early March. Likewise, thickness of the longissimus dorsi muscle (4.3–6.6 cm) of adult cows also suggests considerable variation in nutritional condition (Cook 2000).

Lactational status significantly affected variation in body fat, the only variable in our analysis to do so. Nonlactating cows

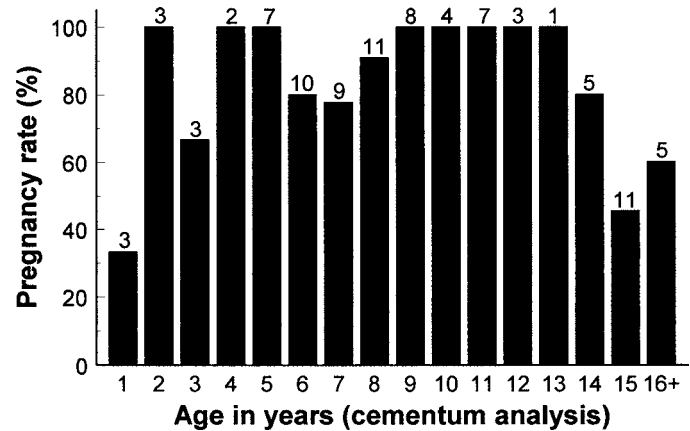


FIG. 6.—Pregnancy rates by age for northern Yellowstone cow elk in 2001–2002. Sample sizes for each age class are shown above bars.

were twice as fat as cows that were lactating at the time of capture and had 40% more body fat than cows with a remnant udder (i.e., previously lactating). Such trends have been reported for elk (Stussy 1993; Trainer 1971) and attest to the considerable nutritional demands of lactation (Cook 2002; Oftedal 1985; Verme and Ullrey 1984).

Body fat was unrelated to age. This counters Flook's (1970) findings that, at least in late autumn and early winter, cow elk >10 years old in the Canadian Rockies had less body fat reserves (kidney fat) than did younger adults. Winter kidney fat and gutted carcass mass of red deer in Scotland (Clutton-Brock et al. 1982; Mitchell et al. 1977) followed a trend similar to that described by Flook (1970). In our study, reduced frequency of pregnancy in older cows might allow them to maintain higher mean body fat levels than if they reproduced at the same rate as prime-aged cows.

Other factors also could contribute to differences in body fat levels among elk. Body condition might vary with microclimatic conditions and snow depth across the winter range (DelGiudice et al. 2001; Houston 1982). We avoided an analysis based on microclimate because we could not correlate specific conditions to individual elk for the winter period prior to their capture. Forage quality and quantity across the summer range undoubtedly vary and could account for some of this variation (Hobbs 1989) because body fat accretion, particularly of lactating elk, over summer–autumn is sensitive to digestible energy content of diets (Cook et al. 2004). Body fat levels at the end of winter the year previous to capture might have influenced body fat levels at the time of capture as well. Assessing these factors would require monitoring of individual elk sequentially across multiple seasons.

Evaluating the implications of our body condition data to population dynamics of YNP elk is constrained because very little body fat data from wild elk suitable for comparison have been published. Stussy (1993) reported body fat of 3.5% for lactating ($n = 29$) and 7.4% for nonlactating ($n = 22$), hunter-killed Roosevelt elk (*C. e. roosevelti*) in western Oregon in January and February 1988–1989, substantially lower than levels in YNP (5.8% and 11%, respectively). Flook (1970)

indicated body fat levels of 12.2% (8.5–14.8%) for 6 adult Rocky Mountain cow elk in Canada, but these data were collected in early winter and lactational status was not reported, thereby hindering comparison with our data. (Both studies presented kidney fat data that we converted to body fat by the equations of Cook et al. [2001a]).

Research with captive elk indicates several important thresholds of body fat relevant to survival and reproduction (Cook et al. 2004) and could provide some insight into the significance of the body fat levels that we documented. Body fat accretion during summer significantly influences probability of overwinter survival (Hobbs 1989). In harsh winter weather, survival probability is much greater if cow elk leave the summer range with $\geq 15\%$ body fat, and survival probability declines at prewinter fat levels $< 10\%$ (Cook et al. 2004). Good to excellent forage during summer should result in body fat $\geq 15\%$ in lactating cows during autumn. Such conditions also support rapid growth and development of calves, which in turn significantly enhance their survival probability in harsh winters (Cook et al. 2004). Elk with body fat levels $\geq 5\%$ late in winter should have an excellent chance of surviving as long as harsh winter weather moderates at this time. Probability of succumbing to harsh weather and submaintenance diets greatly increases at $\leq 2\%$ body fat. Such a level, especially in early winter, would be suggestive of elk highly prone to starvation death depending on winter severity. Probability of breeding declines markedly as autumn body fat declines below about 9% (10–11% for wild Oregon elk—Kohlmann 1999), and breeding is unlikely at $< 6\%$ body fat. In addition, breeding can be delayed in adult cows with $< 13\%$ body fat (Cook et al. 2004).

Northern Yellowstone cow elk appeared in relatively good condition for mid- to late winter. Only 4% of cows were at a level of condition ($\leq 2\%$ fat, equivalent to femur fat $\leq 40\%$ —Cook et al. 2001a; thickness of longissimus dorsi muscle < 4.5 cm, which indicates elevated protein catabolism—Cook 2000) at which probability of mortality due to winter starvation might be relatively high (Fig. 3). Most (85%) possessed at least 5% body fat (equivalent to femur fat levels of $> 85\%$ —Cook et al. 2001a) during February–March, indicating good to excellent survival probability through the rest of winter (Cook et al. 2004).

Despite the relatively high levels of late winter body fat for YNP cow elk, our data suggest that some nutritional limitations might have occurred on summer ranges during the study. The marked differences in body fat between lactating and nonlactating cows imply that digestible energy intake was insufficient to support both lactation and fat accretion at the apparently high rate of the nonlactating cows during summer and autumn. In captive elk, lactating cows with access to high-quality forage (> 2.8 kcal digestible energy/g) accrue body fat at a rate similar to that of nonlactating cows during summer and autumn. Fat accretion declines to a significantly greater extent in lactating compared with nonlactating cows as digestible energy intake in summer and autumn declines, reflecting the elevated greater nutritional requirements imposed by lactation (Cook et al. 2004). In wild red deer, Clutton-Brock et al. (1983) reported similar findings, in that fertility, and presumably body

fat, of lactating hinds declined significantly but remained high for nonlactating hinds as population density increased. Alternatively, lactation during winter might account for observed differences in body fat between lactating and nonlactating cows. However, Robbins et al. (1981) argued that milk yields after mid-autumn are too low to appreciably affect energy balance. Finally, the high pregnancy rate of YNP prime-aged cows (91%) is not necessarily indicative of excellent summer–autumn nutritional conditions (Cook et al. 2004). These high pregnancy rates indicate only that body fat during breeding is $\geq 8\text{--}9\%$. This level ($< 10\%$ body fat) is far below what cow elk can achieve (15–20%—Cook et al. 2004) if summer–autumn forage conditions are good to excellent and is indicative of summer–autumn nutrition that would reduce calf growth and thus predispose them to increased overwinter mortality (Cook et al. 2004). Moreover, high calf mortality during the 1st few months after parturition, such as that reported in YNP (35%—Singer et al. 1997), would tend to increase overall herd fat levels and pregnancy rates despite marginal summer–autumn nutrition (Verme and Ullrey 1984).

Probability of pregnancy for YNP elk during mid- to late winter followed a logistic curve as a function of body fat (Fig. 4) that is typical (though shifted to the left) of that for captive elk during the breeding season (Cook et al. 2004; Fig. 4) and of those presented for caribou (*Rangifer tarandus*—Gerhardt et al. 1997) and moose (*Alces alces*—Heard et al. 1997; Testa and Adams 1998). The higher pregnancy rate across any given level of body condition of Yellowstone elk, compared with captive elk, probably is due to fat catabolism between the breeding season and late winter.

Our data indicate that failure of cow elk to breed was a function of their fat levels; most of these elk were either lactating or > 14 years old. Much of the literature on age–fertility relations in temperate zone ungulates shows decreased productivity as females age (Eberhardt 1985; Ericsson et al. 2001; Houston 1982), as in this study (91% pregnancy for cows 4–14 years old and 50% for cows > 14 years old). However, our analysis indicated that body condition, rather than age, directly accounted for probability of pregnancy. As body condition declined, probability of pregnancy declined independently of age (Fig. 4). Reduced rates of pregnancy in older cows possibly was due to their reduced ability to maintain or recover energy reserves if they raised a calf, perhaps due to normal wearing of teeth (Laws 1981; Shupe et al. 1984).

The age segregation we observed (Fig. 2), although not reported before for these elk, suggests that sampling to ensure a truly unbiased estimate of age, and other variables that covary with age (e.g., pregnancy and lactation proportions), requires careful attention to sampling strategy. Our capture effort might not represent an unbiased sample for the entire northern Yellowstone herd, particularly because it did not include cows outside the park boundary, where younger elk might be relatively more abundant. A truly randomized sampling approach (for an area as extensive as the northern range of Yellowstone) has the potential for greatly increasing capture costs. It might also require sampling inside and outside of the park in proportion to the number of elk in each area.

We could not address another potential source of bias resulting from spatial segregation by lactational status previously noted for this herd (i.e., cows with calves tend to be relatively more abundant at the western portion of the winter range—Coughenour and Singer 1996a:580; Houston 1982) because our sample of lactating cows was too small. Such spatial segregation has the potential to bias nutritional condition data given the significant differences in body fat levels between lactating and nonlactating cow elk in our sample. However, nutritional condition estimates, when stratified by lactational status, avoids this problem to a large degree.

Our body fat data reflect winters that ranged from mild to normal and growing season precipitation that ranged from below to above average. Under these conditions, we conclude that levels of body fat appear to be sufficiently high to preclude appreciable overwinter mortality of adult cows. DelGiudice et al. (2001) also reported that the magnitude of negative energy balance (evaluated with urinary indices) was too small to induce appreciable mortality of cows and calves in the northern herd during mild to normal winters.

Although based on circumstantial evidence, our body fat analyses suggest the possibility of nutritional limitations occurring on the summer range. This possibility counters the long-held belief that nutrition during summer–autumn is not an important limiting factor of elk in YNP (Coughenour and Singer 1996b) or in other areas (e.g., see Lyon 1980; Nelson and Leege 1982; Unsworth et al. 1998). However, nutritional demands of lactating females and their offspring are markedly higher during summer–autumn than winter (Cook 2002; Haigh and Hudson 1993; Oftedal 1985; Parker et al. 1999), and there is supporting evidence from the park (Merrill and Boyce 1991) and elsewhere (e.g., Alldredge et al. 2002; Cook 2002; Cook et al. 1996, 2004; Julander et al. 1961; Klein 1970; Parker et al. 1999; Sæther and Heim 1993; Trainer 1971; Verme and Ullrey 1984) that cautions against dismissing the possibility of summer nutritional limitations without rigorous empirical evidence.

Population dynamics of northern YNP elk are greatly influenced by occasional severe winters (Coughenour and Singer 1996b), and our data do not refute this. Rather, our data suggest an interaction hypothesis: the cumulative effect of nutrition on the herd over the long-term might result from interactions between relatively acute, but infrequent, effects of nutrition on survival during harsh winters and small to moderate chronic effects of nutrition in summer and autumn on reproduction and survival (including predisposing effects originating on summer range that are not manifested until winter, e.g., reduced calf growth in summer that reduces their survival in winter—Merrill and Boyce 1991). Testing this hypothesis and clarifying the relative contributions of summer–autumn versus winter nutrition will be challenging. However, determining body fat of cows and size and condition of calves in autumn would be a useful 1st step that would better identify the need for a more intensive effort.

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