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Body condition and pregnancy in northern Yellowstone elk: Evidence for predation risk effects?

P. J. White,[1,5] Robert A. Garrott,[2] Kenneth L. Hamlin,[3] Rachel C. Cook,[4]
John G. Cook,[4] and Julie A. Cunningham[3]

[1]*National Park Service, P.O. Box 168, Yellowstone National Park, Wyoming 82190 USA*
[2]*Fish and Wildlife Management Program, Department of Ecology, Montana State University, Bozeman, Montana 59717 USA*
[3]*Montana Fish, Wildlife, and Parks, 1400 South 19th Avenue, Bozeman, Montana 59718 USA*
[4]*National Council for Air and Stream Improvement, 1401 Gekeler Lane, La Grande, Oregon 97850 USA*

Abstract. S. Creel et al. reported a negative correlation between fecal progesterone concentrations and elk : wolf ratios in greater Yellowstone elk (*Cervus elaphus*) herds and interpreted this correlation as evidence that pregnancy rates of elk decreased substantially in the presence of wolves (*Canis lupus*). Apparently, the hypothesized mechanism is that decreased forage intake reduces body condition and either results in elk failing to conceive during the autumn rut or elk losing the fetus during winter. We tested this hypothesis by comparing age-specific body condition (percentage ingesta-free body fat) and pregnancy rates for northern Yellowstone elk, one of the herds sampled by Creel et al., before (1962–1968) and after (2000–2006) wolf restoration using indices developed and calibrated for Rocky Mountain elk. Mean age-adjusted percentage body fat of female elk was similarly high in both periods (9.0% ± 0.9% pre-wolf; 8.9% ± 0.8% post-wolf). Estimated pregnancy rates (proportion of females that were pregnant) were 0.91 pre-wolf and 0.87 post-wolf for 4–9 year-old elk (95% CI on difference = –0.15 to 0.03, $P = 0.46$) and 0.64 pre-wolf and 0.78 post-wolf for elk >9 years old (95% CI on difference = –0.01 to 0.27, $P = 0.06$). Thus, there was little evidence in these data to support strong effects of wolf presence on elk pregnancy. We caution that multiple lines of evidence and/or strong validation should be brought to bear before relying on indirect measures of how predators affect pregnancy rates.

Key words: Canis lupus; Cervus elaphus; *condition; elk; nutrition; predation; pregnancy; wolves; Yellowstone*.

Introduction

Many ecologists have become interested in the consequences of antipredator strategies employed by prey in response to predation risk. Understanding these consequences is important because they can enhance or obscure consumptive effects on prey population growth, life history, and resource use (Preisser and Bolnick 2008). Creel et al. (2007) suggested that pregnancy rates of elk (*Cervus elaphus*) in the greater Yellowstone ecosystem, as determined indirectly through measurement of average fecal progesterone levels, decreased in the presence of wolves (*Canis lupus*). This apparent effect was attributed to changes in foraging patterns of elk that carried nutritional costs rather than changes in glucocorticoid concentrations due to stress (Creel et al. 2009, Christianson and Creel 2010). The possibility that antipredator strategies to avoid being killed by wolves could decrease forage intake (nutrition) and reproductive rates of elk is intriguing and has major implications for predicting the outcomes of predator–prey interactions in large mammal systems (Creel and Christianson 2008).

Studies with both captive and free-ranging elk have demonstrated a strong correlation between pregnancy and body fat in autumn. The probability of becoming pregnant decreases significantly as body fat during the breeding season decreases below 9–11% and decreases markedly at <6% body fat (Kohlmann 1999, Cook et al. 2004*a*). Likewise, the probability that elk are pregnant in mid- to late winter follows a logistic curve as a function of body fat (Cook et al. 2004*b*). Thus, the hypothesized mechanism for lower pregnancy rates in elk as a consequence of antipredator responses that carry nutritional costs is that reduced body condition (fat, protein) results in (1) elk not conceiving due to low body fat during the autumn breeding season, (2) elk conceiv-

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[5] E-mail: pj_white@nps.gov

ing but losing the fetus due to inadequate winter nutrition and inadequate progesterone levels to maintain pregnancy, or (3) some combination of both (Creel et al. 2007, 2009).

To prevent elk from accruing enough body fat to get pregnant, elk antipredator behavioral responses to wolves would have to result in limited forage intake or force elk into areas of lower forage quality during spring and summer. However, forage abundance and quality, and the spatial extent and availability of foraging areas, is highest during late spring through mid-autumn on montane ranges of the Rocky Mountain region (Merrill and Boyce 1991). Both elk and wolves are distributed over larger areas and are at much lower densities than during winter and, therefore, it is likely that wolves are less able to keep elk from accessing forage during summer than in winter. For example, northern Yellowstone elk migrate away from the most concentrated area of wolf activity during summer, when wolf activity is centered around dens and rendezvous sites, and select habitats at higher elevations that allow them to obtain abundant, nutritious forage (Mao et al. 2005).

For wolf presence to cause reduced body fat in elk that induces reproductive failure, it is usually hypothesized that wolves would have to limit nutrient intake (nutrition) by elk during winter when elk concentrate on ranges where forage availability and quality are typically limited (Creel et al. 2007). Elk in the greater Yellowstone ecosystem often cannot separate themselves from wolves during winter, but rely on other behaviors to reduce predation risk (Mao et al. 2005). However, assessments of elk antipredator strategies during winter have been ambiguous regarding whether wolves cause elk to avoid favored foraging areas, decrease time spent foraging, and decrease nutrition (Creel et al. 2005, Fortin et al. 2005, Kauffman et al. 2007, Gower et al. 2009*a*, *b*, White et al. 2009).

We tested the Creel et al. (2007, 2009) hypothesis by comparing direct measures of age-specific body condition (percentage ingesta-free body fat) and pregnancy rates for northern Yellowstone elk, one of the herds sampled by Creel et al. (2007; Blacktail Plateau), before (1962–1968) and after (2000–2006) wolf restoration. The northern Yellowstone elk population spends winter on grasslands and shrub steppes along the northern boundary of Yellowstone National Park and nearby areas of southwest Montana (Houston 1982). Wolves were restored to the Park in 1995–1996 and their abundance and distribution rapidly increased to the extent that they were considered biologically recovered by 2002 (Smith 2005).

METHODS

During 1930–1968, staff from Yellowstone National Park (USA) removed 26 403 northern Yellowstone elk due to concerns about overgrazing, while hunting outside the Park removed another 44 927 elk (Houston 1982). As a result, elk counts decreased from ~12 000 in 1933 to an average of 4400 elk (SD = 1124) on the winter range during 1962–1968. Thus, nutrition and body condition of northern Yellowstone elk during the 1962–1968 pre-wolf sampling period should have been relatively high given that they were sampled when elk counts were far below the estimated ecological carrying capacity of 15 000 (Houston 1982), and per capita resource availability should have been quite high. The pre-wolf data were collected from 431 adult female elk >3 years old trapped and culled from Yellowstone National Park during February and March, 1962–1968, by biologists from the National Park Service and Montana Fish and Game Department (e.g., Greer 1968). Age was estimated by tooth eruption patterns or wear in 1-year increments for yearlings through 9-year-olds. Older animals were estimated to be 10–15 years old or >15 years old. Pregnancy status was assessed by examining the reproductive tracts for the presence of a fetus. Also, the mass of fat attached to each kidney was measured for a subsample of 91 of these elk. We used the natural logarithm of the average fat mass of the paired kidneys (Anderson et al. 1972) in the regression equation developed for female Rocky Mountain elk to estimate ingesta-free percentage body fat ($y = 4.573x - 13.050$; $R^2 = 0.86$; Cook et al. 2001*a*).

The northern Yellowstone elk population expanded their winter range north of the Park and into the Yellowstone Valley of Montana during the 1970s and 1980s in response to increasing elk abundance, changes in the structure and timing of hunter harvests, and protection of winter ranges outside the Park (Coughenour and Singer 1996, Lemke et al. 1998). Thus, the estimated carrying capacity increased to between 20 000 and 25 000 elk (Taper and Gogan 2002). In addition, extensive fires during 1988 burned approximately one-third of the winter and summer ranges for northern Yellowstone elk (Despain et al. 1989, Singer et al. 1989). However, these fires mostly burned sage-steppe grasslands, and fire-induced increases in forage productivity and quality were no longer detectable five years after the fires (Singer and Harter 1996). Thus, while elk counts during the 2000–2006 post-wolf sampling period were triple that of the pre-wolf period, averaging 13 300 (SD = 1288; Eberhardt et al. 2007), the population was still well below the estimated carrying capacity. During the post-wolf sampling period wolf numbers on the northern range were among the highest densities reported in the literature (mean = 43 wolves per 1000 km^2; Smith 2005), and the region was also experiencing extreme drought conditions that reduce forage quality and quantity (White et al. 2008).

During the post-wolf sampling period (2000–2006), 139 adult female elk >3 years old were captured in February and March via helicopter net-gunning (Hawkins and Powers, Greybull, Wyoming; Leading Edge Aviation, Lewiston, Idaho). Age was estimated using cementum analysis of an extracted vestigial canine tooth (Hamlin et al. 2000), and pregnancy was determined from a serum sample using the pregnancy-specific protein B assay (BioTracking, Moscow, Idaho, USA; Sasser et al. 1986, Noyes et al. 1997). In addition, we evaluated nutritional condition for 77 elk of our sample (Cook et al. 2004*b*) during 2000–2002 via a rump body condition score developed for elk and maximum subcutaneous rump fat thickness (Cook et al. 2001*a*, *b*) measured using a Sonovet ultrasonagraph with a 5.0-MHz, 7.0-cm probe (Universal Medical Systems, Bedford Hills, New York, USA). We also measured chest-girth circumference and converted our hobbled circumference measurements (x) to a sternally recumbent basis (y), using the equation $y = 0.88x + 15.39$ (Cook et al. 2003), prior to calculation of body mass. We estimated ingesta-free body fat percentage using the scaledLIVINDEX for elk, which is an arithmetic combination of the rump body condition score and maximum rump fat thickness allometrically scaled using body mass (Cook et al. 2010). This research was part of a comparative study of percentage ingesta-free body fat in late winter and early spring for female elk from 19 populations across the northwestern United States (Cook et al. 2010).

Because pregnancy rates in young and senescent elk are lower than that of mature elk (Cook et al. 2004*b*), we partitioned the data with three age classes: <4 years old, 4–9 years old, and >9 years old. We censored data for the <4 years old elk due to low sample sizes ($n = 8$) of elk sampled for body fat during the 2000–2006 period. We calculated estimates and 95% confidence intervals (CI) for ingesta-free body fat for the two age classes (4–9 years old, >9 years old) during the 1962–1968 pre-wolf period ($n = 91$) and the 2000–2006 post-wolf period ($n = 77$). We also calculated estimates and 95% confidence intervals for the observed proportions of pregnant elk in the two age classes during the 1962–1968 pre-wolf period ($n = 431$) and the 2000–2006 post-wolf period ($n = 139$). We calculated the difference in mean body fat and observed proportions of pregnant elk between the pre- and post-wolf periods for the two age classes and used continuity-corrected 95% Wald's confidence intervals to evaluate potential changes in body fat and pregnancy rates between the sampling periods. We used the t test to compare mean body fat of the pre- and post-wolf samples for each age class and the z test to compare observed proportions of pregnant elk in pre- and post-wolf samples for each age class. We consider a difference significant if $P \leq 0.10$.

RESULTS

The mean midwinter ingesta-free body fat estimates for 4–9 year-old elk were 10.3% ($n = 61$, SD = 3.97, 95% CI = 9.3–11.3, and 9.4% ($n = 42$, SD = 3.34, 95% CI = 8.4–10.4) for the pre- and post-wolf periods, respectively. The mean midwinter ingesta-free body fat estimates for >9-year-old elk were 6.5% ($n = 30$, SD = 4.16, 95% CI = 5.0–8.0) and 8.3% ($n = 35$, SD = 3.62, 95% CI = 7.0–9.5) for the pre- and post-wolf periods, respectively. The mean body fat of 4–9 year-old elk in the post-wolf sample was similar to the mean of the pre-wolf sample (diff = −0.9%, 95% CI = −2.36 to 0.56, $P = 0.26$), while the mean body fat of >9-year-old elk in the post-wolf sample was higher than the mean of the pre-wolf sample (diff = 1.76, 95% CI = −0.13 to 3.65, $P = 0.07$). Across all age classes of elk sampled during the pre-wolf period, 59% had >7.5% body fat during midwinter, suggesting a probability of pregnancy >80% (Cook et al. 2004*b*), while 23% had <4.8% body fat, suggesting <50% probability of pregnancy. Two-thirds of these latter elk were yearlings or elk >15 years old. For the post-wolf period, 69% of elk had >7.5% body fat, suggesting a probability of pregnancy >80%, while only 14% had <4.8% body fat suggesting <50% probability of pregnancy. The mean midwinter body fat levels of northern Yellowstone elk during the post-wolf period were among the highest body fat levels measured in 19 herds across the western United States (Fig. 1).

Observed pregnancy rates for elk 4–9 years old were 0.91 ($n = 325$, 95% CI = 0.87–0.94) and 0.87 ($n = 62$, 95% CI 0.76–0.94) for the pre- and post-wolf samples, respectively. Observed pregnancy rates for elk >9 years old were 0.64 ($n = 106$; 95% CI = 0.54–0.73) and 0.78 ($n = 77$; 95% CI = 0.67–0.87) for the pre- and post-wolf samples, respectively. The observed pregnancy rate of 4–9 year old elk in the post-wolf sample was similar to the observed pregnancy rate in the pre-wolf sample (diff = −0.04, 95% CI = −0.15 to 0.03, $P = 0.46$) while the observed pregnancy rate of >9-year-old elk in the post-wolf sample was higher than that observed in the pre-wolf sample (diff = 0.14, 95% CI = −0.01 to 0.27, $P = 0.06$).

DISCUSSION

There was little evidence in the data to support the Creel et al. (2007, 2009) hypothesis of strong nutritional costs from antipredator responses inducing substantial decreases in pregnancy rates for northern Yellowstone elk in the presence of wolves. The data indicated that the body fat of northern Yellowstone elk during late winter was similar between the pre-wolf and post-wolf sampling periods and likely sufficient to preclude appreciable susceptibility to late winter/early spring starvation-induced fetal mortality (Cook et al. 2004*a*, *b*). Indeed, the mean late winter body fat of adult females in the post-wolf sample was among the highest recorded in a comparative study of 19 elk herds, despite coinciding with one of the highest densities of wolves reported for North America (Fuller et al. 2003, Smith 2005), while wolves were absent on the ranges of the majority of the other herds sampled. The relatively high late winter body fat levels documented in both the pre- and post-wolf samples are consistent with our findings that the observed proportions of adult female elk that were pregnant in the presence of wolves were similar to or higher than prior to wolf restoration.

Creel et al. (2007) proposed the hypothesis that wolf presence decreased pregnancy rates of elk based on

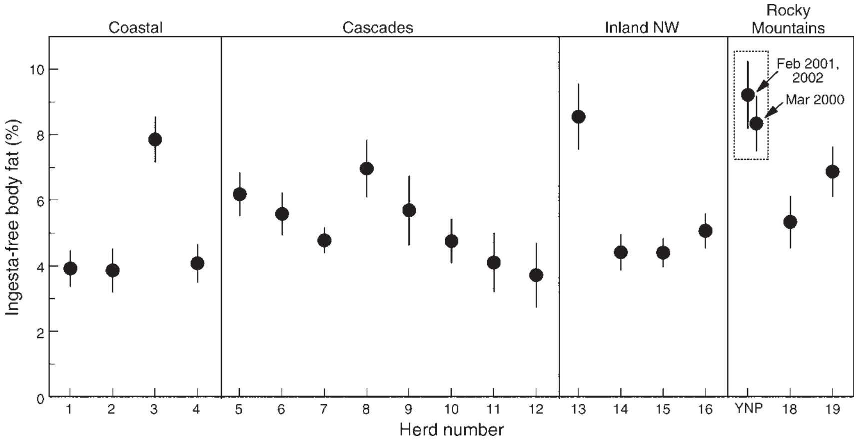

FIG. 1. Average percentage of ingesta-free body fat in late winter and early spring for female elk (*Cervus elaphus*) in 19 herds across four regions of the western United States. Body fat was estimated using the scaledLIVINDEX for elk, a combination of ultrasonography of maximum subcutaneous rump fat thickness and the rump portion of a body condition score. All data were collected between February and early April during 1998–2007, and typically included two years of sampling (range 1–7) and 40 sampled elk (range 11–160) per herd (see Cook et al. [2010] for descriptions of this data set). The dotted rectangle delineates Yellowstone National Park (YNP) data. Error bars represent ±2 SE.

average progesterone concentrations in late winter fecal samples collected from four elk winter ranges. Creel and Christianson (2008), Creel et al. (2009), and Christianson and Creel (2010) attributed the effect of wolf presence on elk reproduction to changes in foraging patterns that carry nutritional costs rather than changes in glucocorticoid concentrations (stress) and proposed the effects were strong and ubiquitous in elk–wolf systems. However, we recommend caution in interpreting and generalizing the Creel et al. (2007) results for several reasons. First, comparisons within and among areas of mean progesterone levels derived from simple random collections of fecal pellets along tracks in the snow could be biased by collecting a variable and unknown proportion of samples deposited by immature or male elk (White et al. 1995*b*). Second, Creel et al. (2007) inferred pregnancy rates from ratios of calves per 100 cows in the subsequent year, which is a tenuous assumption as low recruitment could be related to low calf survival. Third, the positive regression relationships presented by Creel et al. (2007) between calf recruitment in the subsequent year and elk–wolf ratios or mean fecal progesterone concentrations resulted from differences among sample collection areas (winter ranges) rather than within areas. Elk–wolf ratios and progesterone concentrations were not strongly correlated with calf recruitment in the subsequent year for any of the sampled winter ranges, despite relatively large within-area variations in both elk–wolf ratios and progesterone concentrations over the study (see Fig. 1b, c in Creel et al. 2007).

Furthermore, independent studies of the same elk populations and time periods sampled by Creel et al. (2007) found that post-wolf pregnancy rates were equal to or higher than pre-wolf pregnancy rates based on observations of fetuses from hunter-harvested elk and pregnancy-specific protein B assays of blood samples (Hamlin et al. 2009). Pregnancy-specific protein B assays are the definitive standard for nonlethal pregnancy assessment in elk (Sasser et al. 1986, Noyes et al. 1997). Pregnancy rates in these independent studies were not significantly related to numbers of wolves or elk–wolf ratios (Hamlin et al. 2009). Likewise, high pregnancy rates were reported for elk exposed to relatively high and consistent wolf predation in Idaho (Zager et al. 2007) and Banff, Jasper, and Riding Mountain national parks in Canada (P. Paquet, *personal communication*). In addition, annual mean masses recorded for 1906 northern Yellowstone elk calves harvested after wolf restoration were at or above the annual mean masses recorded during the decade prior to wolf restoration, suggesting no wolf-induced decreases in nutrition (Hamlin et al. 2009).

The fecal progesterone methodology for assessing pregnancy in elk was initially developed and tested by two of the authors of this article using radio-collared adult female elk in the Madison headwaters of Yellowstone (White et al. 1995*a*, Garrott et al. 1998), and validated with captive female elk by Cook et al. (2002). However, subsequent assays of feces collected from this elk herd in some pre- and post-wolf years revealed substantial errors of misclassifying pregnant animals as nonpregnant based on observations of calves with marked females and population measures of calf production (Garrott et al. 2003, 2009*a*). Many of these fecal samples were assayed in the same laboratory and frequently intermixed with the fecal samples reported in Creel et al. (2007). We suspect there is some unexplained failure of the fecal hormone assays for progesterone under certain circumstances such as the physiological binding of metabolic by-products of progesterone in the gut or interference by them such that progesterone was not recognized in the radio and enzyme immunoassays (Garrott et al. 2003, 2009*b*, Hamlin et al. 2009). However, we have been unable to explain the aberrant fecal steroid results despite additional assay work and numerous consultations with biologists and reproductive endocrinologists (S. Creel and J. Berardinelli, Montana State University; S. Monfort, Smithsonian Institution). Thus, we urge caution in using the fecal progesterone technique until further work resolves inconsistencies.

Despite these criticisms and disparate findings, we encourage continued site-specific investigations of the relative influences of habitat conditions and antipredator responses on the body condition and probability of pregnancy in elk because, theoretically, the consequences of antipredator responses that carry nutritional costs could approach the consequences of direct predation (Creel and Christianson 2008, Peckarsky et al. 2008). Future studies should consider factors in addition to predation that could lower pregnancy rates in elk, including climate and forage conditions (Peckarsky et al. 2008), an aging population (White and Garrott 2005), interactions among nutrition, condition, and lactation (Cook et al. 2004*a*, *b*), low breeding bull : female ratios (Raedeke et al. 2002), and diseases such as brucellosis (Geremia et al. 2009, Rhyan et al. 2009) that are increasing in prevalence in some areas (Cross et al. 2010). The Yellowstone wolf saga has become an exemplar of the ecological consequences of large predator restoration, which is likely to guide science and policy regarding such intentional introductions. Thus, it is imperative that multiple lines of evidence and/or strong validation be brought to bear when assessing the effects of antipredator responses on elk demographic rates.

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