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We related annual and seasonal survival of four populations of elk *Cervus elaphus* in the Pacific Northwest, USA, to measures and indices of individual nutritional condition. Among populations, for all mortality (human and non-human causes) sources inclusive, annual survival of adult females was correlated with a rump body condition score ($r_s = 0.627$, $P = 0.071$), and survival over spring-summer-autumn (SSA) was correlated with mean ingesta-free body fat (IFBF; $r_s = 0.567$, $P = 0.088$) and rump body condition score (rBCS; $r_s = 0.615$, $P = 0.050$). For non-human mortality sources only, survival through SSA was correlated with IFBF ($r_s = 0.567$, $P = 0.088$) and rBCS ($r_s = 0.615$, $P = 0.050$), and survival over winter was correlated with withers body condition score ($r_s = 0.677$, $P = 0.045$). For human-caused mortality sources only, survival over SSA was correlated with rBCS ($r_s = 0.696$, $P = 0.036$) and IFBF ($r_s = 0.696$, $P = 0.036$). For individuals, logistic analysis found that individual likelihood of dying from all mortality sources inclusive was best predicted ($\chi^2 = 8.3$, $P = 0.004$, $\beta = -1.24$) by *longissimus dorsi* (loin) muscle thickness, a measure of protein catabolism. For only non-human mortality sources, a model ($\chi^2 = 16.1$, $P = 0.0003$) containing both loin muscle thickness ($\chi^2 = 5.7$, $P = 0.017$, $\beta = -1.02$) and percent ingesta-free body fat ($\chi^2 = 4.9$, $P = 0.027$, $\beta = -0.35$) best predicted individual susceptibility to mortality. Odds ratios indicated that odds of dying increased approximately 3X for each centimeter of loin muscle catabolized and 1.4X for each percent less body fat. No condition indices at the individual level were related to survival from human-caused mortality sources. Our study populations were characterized by low-marginal condition (i.e. mean ingesta-free body fat levels of 5.9-12.3% for lactating cows in late autumn); this likely increased the prominence of measures of muscle catabolism relative to fat accretion in influencing individual elk survival. Elk populations throughout the Pacific Northwest likely show similar condition levels, and consequently individuals are predisposed to mortality to a much greater degree than under optimal foraging conditions. Management strategies which assume that nutritional condition affects vulnerability only at or near condition levels associated with ecological carrying capacity (i.e. near starvation mortality) may overestimate the impact of proximate mortality factors on adult female elk.

Key words: cause-specific mortality, Cervus elaphus, condition, elk, ingesta-free body fat, mortality, nutrition, nutritional condition, survival

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Ungulate populations are thought to respond to resource limitations through a predictable process, i.e. declines in juvenile fecundity, juvenile survival, adult fecundity and lastly adult survival (Gaillard et al. 2000, Eberhardt 2002). These parameters are fundamentally related to individual nutritional condition (Clutton-Brock et al. 1982, Verme & Ullrey 1984, National Research Council 1985, 1996, Whitten et al. 1992, Adams et al. 1995, Sams et al. 1996, Keech et al. 2000, Cook et al. 2004). Although effects of resource limitations (depressed condition) on adult survival would be most pronounced at or near ecological carrying capacity (Gaillard et al. 2000, Eberhardt 2002), poor condition may predispose individuals to various mortality factors even at lower densities due to effects on alertness, fleeing ability and immuno-competence (Hanks 1981, Davidson & Doster 1997, Bender & Hall 2004). Hanks (1981) first postulated a relationship between nutritional condition and demographic vigour (fecundity and survival rates) in populations. Several studies have subsequently looked for relations between condition and survival in elk and red deer *Cervus elaphus*, particularly as related to predation (Huggard 1993, Kunkel & Pletscher 1999, Gula 2004), but most of these have been hampered by use of condition indices that were invalid or of limited value in predicting individual nutritional condition (Cook et al. 2001).

Elk numbers and productivity of some herds in the Pacific Northwest (PNW) of the United States have been declining for decades (Noyes et al. 2002, Washington Department of Fish and Wildlife 1997). Causes of these declines are unknown, but hypotheses include decreasing forage conditions, increased predation and low adult sex ratios (Noyes et al. 2002). Empirical data for any of these hypotheses are lacking, although adult sex ratios appear to have little effect on elk productivity (White et al. 2001, Bender 2002, Bender et al. 2002b). A growing body of evidence indicates strong relations between condition of elk and fecundity, juvenile survival and productivity rates in free ranging (Clutton-Brock et al. 1982, Bender & Cook 2005, Bender et al. 2006) and captive (Cook et al. 1996, 2004) populations. Because of the high elasticity of adult female survival on population rate of increase (Gaillard et al. 2000, Eberhardt 2002) it is important to determine whether condition affects adult survival under typical conditions for free ranging elk in the PNW.

Our goal was to evaluate the influence of nutritional condition on survival of adult female elk in the PNW. Our specific objectives were to: 1) determine nutritional condition of adult female elk in four populations covering the range of habitat conditions available to elk in the PNW, 2) determine survival rates and causes of mortality of adult female elk, and 3) determine whether measures or indices of nutritional condition were important in predicting vulnerability of individual elk to mortality. We hypothesized that as individual nutritional condition in populations declined, survival rates would decline and individual adult females would be increasingly predisposed to mortality. Further, measures or indices of condition would be significant predictors of whether individual adult female elk lived or died.

Material and methods

Study area

Our study populations were four geographically distinct elk populations occurring west of the Cascade crest in Washington and Oregon, USA (Fig. 1). The Nooksack herd area covers approximately 1,275 km^2 in the Northern Cascades Physiographic Province of northern Washington, primarily in the cedar *Thuja*-hemlock *Tsuga*-Douglas-fir *Pseudotsuga menziesii* forest type (Küchler 1964, Franklin & Dyrness 1973; see Fig. 1). Dominant species were Douglas-fir with lesser amounts of western hemlock *Thuja heterophylla* and Pacific silver fir *Abies amabilis* at higher elevations. Characteristic species of riparian habitats are red alder *Alnus rubra* and big-leaf maple *Acer macrophyllum*. Land-use in the Nooksack herd area is primarily timber production associated with private industrial forests and state of Washington ownerships. Elevations in the Nooksack herd area ranged from 61 m in the Skagit River valley to 3,347 m a.s.l. at the summit of Mt. Baker. Most of the herd area is in low to mid-elevation mountainous terrain.
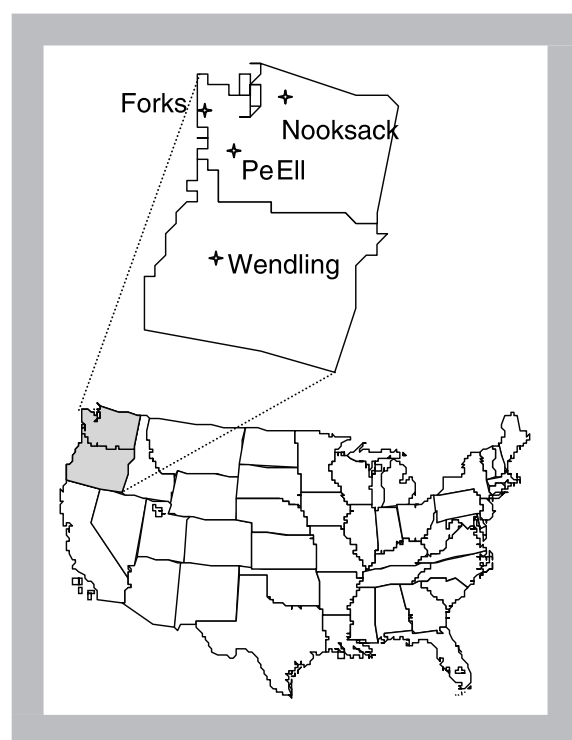

Figure 1. Location of the Nooksack, Forks and Pe Ell, Washington, and of the Wendling, Oregon, study populations.

Climate is characterized by mild wet winters and cool dry summers (Franklin & Dyrness 1973). Precipitation averages approximately 180 cm annually at lower elevations, with 81% falling during October-April, mostly as rain. Average January temperature in the lower elevations of the study area is 2.8°C, while average August temperature is 17.8°C. Snowfall is significant in the higher elevations of our study area. Most elk in the study area are non-migratory, except for a small number that summer in high elevations around Mt. Baker and winter along the Skagit River. Approximately 100 elk of the remnant Nooksack herd occupy the study area, with elk densities being < 0.5/km^2 in the study area. Elk are not legally hunted in the Nooksack area.

The Pe Ell area is located in the Willapa Hills of the Southern Washington Cascade Province, primarily in the cedar-hemlock-Douglas fir forest type (Küchler 1964, Franklin & Dyrness 1973). Topography consists of rolling foothills with steep, high elevation terrain present only in the extreme western portion of the study area. The Pe Ell area is > 80% forested and is dominated by private industrial tree farms of Douglas-fir with lesser amounts of western hemlock. In riparian areas, characteristic species include red alder and big-leaf maple. Climate is maritime with mild wet winters and cool dry summers (Franklin & Dyrness 1973). Precipitation averages 146 cm with 84% falling during October-April. Mean January and August temperatures are 4.4°C and 17.8°C, respectively. Elk are sedentary throughout the study area and the population density in the surrounding game management unit was > 8.0/km^2. Elk hunting seasons consist of primitive weapon and modern firearm seasons, with primitive weapon seasons generally occurring prior to elk captures and modern firearm after. Total harvests during our study were 0.75-1.11 bulls/km^2 and 0.28-0.39 cows/km^2. Harvest strategies were aselective for cow elk, and cow elk harvest was carefully controlled by limiting numbers of harvest permits. Bull hunting was open-entry, but only bulls with ≥ 3 antler points on at least one antler were legal for harvest.

The Forks study area is in the Olympic Peninsula Physiographic Province, primarily within the spruce-cedar-hemlock forest type (Küchler 1964, Franklin & Dyrness 1973). Topography consists of rolling to hilly terrain of the coastal range. Landownership is primarily industrial tree farms of Douglas-fir and western hemlock, with significant

amounts of Sitka spruce *Picea sitchensis* in low lying areas. Climate is maritime with mild wet winters and cool dry summers (Franklin & Dyrness 1973). Precipitation averages 309 cm, with 84% falling during October-April. Low-lying areas are frequently flooded due to high annual precipitation. Mean January and August temperatures are 3.9°C and 16.1°C, respectively. No significant snowfall occurs in the study area. Elk are sedentary in the study area, and population density is approximately $8.0/km^2$ in the surrounding game management units. Elk hunting seasons consist of primitive weapon and modern firearm seasons, with primitive weapon seasons generally occurring prior to elk captures and modern firearm after. Total harvests during our study were 0.28-0.41 bulls/km^2 and 0.10-0.16 cows/km^2. Harvest strategies were aselective for cow elk, and cow elk harvest was carefully controlled by limiting numbers of harvest permits. Bull hunting was open-entry, but only bulls with ≥ 3 antler points on at least one antler were legal for harvest.

The Wendling study area is in the Western Cascades Physiographic Province, primarily within the cedar-hemlock-Douglas fir and silver fir-Douglas fir forest types (Küchler 1964, Franklin & Dyrness 1973). Topography consists of rolling to steep terrain associated with the foothills and Cascade Mountains. Landownership is primarily industrial tree farms of Douglas-fir and western hemlock. Climate is maritime to continental with mild wet winters and cool dry summers (Franklin & Dyrness 1973). Precipitation averages 116 cm, with 82% falling during October-April. Mean January and August temperatures are 3.3°C and 18.9°C, respectively. Significant snowfall occurs in the higher elevations of the eastern portion of the study area. Elk inhabiting the eastern portions are migratory, wintering at lower elevations in the western portions of the study area. Elk population densities in the study area are unknown, but likely < 2.6/km^2. Elk hunting seasons consist of primitive weapon and modern firearm seasons, with primitive weapons seasons generally occurring prior to elk captures and modern firearm after. Total harvests during our study were 0.21-0.23 bulls/km^2 and 0.10-0.13 cows/km^2. Harvest strategies were aselective for both bull and cow elk, and cow elk harvest was carefully controlled by limiting numbers of harvest permits.

Elk capture

We captured and fitted female elk ≥1.5 years old with mortality-sensitive radio-collars (ATS, Isanti, Minnesota, USA), during March 2000 - November 2003 inclusive. We captured elk by aerial darting from a Bell 206B JetRanger using carfentanil citrate and xylazine hydrochloride (3.6 mg carfentanil citrate + 100 mg xylazine/elk). One vestigial upper canine was pulled from each captured elk for *cementum annuli* ageing (Hamlin et al. 2000). Immobilized elk were treated with antibiotics, vitamin E/selenium, vitamin B and an 8-way *Clostridium* bactrain. Following processing, the immobilants were antagonized with 360 mg of naltrexone + 1,000 mg of tolazoline/elk. We attempted to recapture the same radio-collared females each subsequent March and November to maintain individual capture histories. However, additional elk were captured and radio-collared to replace annual mortalities in each population.

Nutritional condition

We estimated percent ingesta-free body fat (IFBF) of female elk at each capture using a live animal index, which combined subcutaneous Rump fat depth measured by an ultrasonograph with a rump body condition score ($R^2 = 0.89$; rLIVINDEX; Cook et al. 2001). Percent IFBF was estimated using IFBF = -7.153 + 7.323*X - 0.989*X^2 + 0.057*X^3, where X = rLIVINDEX, an arithmetic combination of subcutaneous rump fat thickness and the rump body condition score (Cook et al. 2001). We also used individual rump (rBCS) and withers (wBCS) body condition scores (Cook et al. 2001), heart girth and maximum subcutaneous fat depth at the rump (Cook et al. 2001) to index condition. We measured thickness of the *longissimus dorsi* (loin) muscle (Cook et al. 2001) by ultrasound between the 12th and 13th ribs to index protein catabolism (Cook 2000).

We assessed pregnancy in both autumn and spring using ultrasonography and rectal palpation (Bingham et al. 1990). We determined lactation status of each captured female by presence/absence of milk in the udder. Mammary tissue still secreting milk indicates nursing by a calf within 3-11 days, and thus survival of calves to that point (Bender et al. 2002a).

Survival and cause-specific mortality

We monitored radio-collared elk a minimum of once per month from either air or ground. Status of each elk (live, dead, cause of mortality) was determined at relocation. Upon detection of a mortality, cause of death was determined (Roy & Dorrance 1976, Adrian 1996) and assigned to one of the following categories: 1) legal harvest, which included elk taken during an established hunting season, 2) malnutrition, which included elk with < 12% femur marrow fat, 3) wounding loss, which included elk wounded during established elk hunting seasons but not recovered by hunters, 4) illegal kill, which included elk intentionally killed outside of established hunting seasons by humans, 5) non-human, which included predation, disease or other non-human induced mortality, and 6) censored, which included elk for which contact was lost either by radio failure, emigration from the study area, or disappearance of the radio signal for unknown reasons. We considered the proximate cause of mortality as the ultimate cause of mortality for all elk except for non-harvested elk with < 12% femur marrow fat. Femur marrow fat values of < 12% were indicative of acute starvation, and thus malnutrition was considered the ultimate cause of mortality for these elk regardless of proximate causes (Depperschmidt et al. 1987, Ratcliffe 1980). The above categories covered all mortalities examined, and we pooled mortality factors into three categories for analysis: all mortality factors inclusive (all), non-human mortality factors only (non-human), and human-caused mortality factors only (human-caused).

We used the Kaplan-Meier staggered-entry estimator to determine survival of radio-collared elk (Pollock et al. 1989) for both all and non-human mortality only. To calculate survival rates due to non-human mortality sources only, we censored human-caused mortalities. We used logistic regression (Hosmer & Lemeshow 1989) to determine variables influencing seasonal mortality of individual elk. We defined seasons as spring, summer and autumn (SSA) and winter. The SSA season occurred generally from early April to late November, the specific timing beginning immediately after the spring capture and condition assessment (late March - early April) and ending at the end-of-autumn capture and condition assessment (mid-late November). The winter season occurred between the autumn capture and the spring capture. The dependent variable was live/die during the season (SSA or winter) after capture and condition assessment. Predictor variables used to model probability of live/die were area, season, age, current season's lactation status, lactation status previous season, lactation status two years previous, current season's pregnancy status, pregnancy status the previous year, pregnancy status two years previously, wBCS, rBCS, maximum subcutaneous fat thickness, loin muscle thickness, girth, IFBF and IFBF the previous season. We developed individual logistic models for each variable to test for significance of individual variable effects, then used all significant variables in a fully parameterized model and eliminated non-significant variables individually using backward elimination to develop a suite of possible models. We used Akaike and Schwartz information criteria differences > 4 and concordance differences > 5% to eliminate models for final selection.

We also used Spearman rank correlations (Zar 1996) to correlate annual and seasonal survival rates with mean population-level estimates of nutritional condition and condition indices among populations. For each test above, we ran three analyses. The first included all mortality causes (including hunter harvest, wounding losses and illegal kills), the second analysis involved only non-human related mortality causes (e.g. predation, malnutrition and disease), and the third only human-caused mortality (harvest, illegal kills and wounding losses).

Results

We captured, radio-collared and monitored a total of 99 adult females in the four study areas, maintaining an average of 17, 18, 21 and 23 collared females annually for the Nooksack, Wendling, Pe Ell and Forks populations, respectively. For our individual elk analyses, this totaled 258 elk seasons among the four study areas after removal of censored individuals.

Body fat

Levels of IFBF inclusive of lactational status in autumn ranged between 1.8-18.2% ($\bar{x} = 12.9$, SD = 3.1) in Nooksack, 2.9-12.9% ($\bar{x} = 7.2$, SD = 2.6) in Pe Ell, 5.0-17.8% ($\bar{x} = 11.2$, SD = 2.6) in Wendling, and 2.9-14.0% ($\bar{x} = 8.6$, SD = 3.5) in Forks. Body fat levels in spring ranged between 4.0-12.2% in Nooksack ($\bar{x} = 6.1$, SD = 2.1),

Table 1. Mean (± SD) indices of individual health or nutritional condition of elk in the Nooksack, Forks and Pe Ell, Washington, and in the Wendling, Oregon, study areas. In the Area column, A indicates autumn condition assessment and S indicates spring condition assessment. wBCS gives withers body condition score, rBCS the rump body condition score, maxF the maximum subcutaneous rump fat thickness, Loin the thickness of the *longissimus dorsi* muscle and Girth the heart girth circumference.

Area	wBCS	rBCS	maxF (cm)	Loin (cm)	Girth (cm)
Nooksack - A	4.3 (0.3)	3.7 (0.7)	2.28 (0.86)	6.0 (0.4)	160.3 (4.5)
Nooksack - S	3.8 (0.7)	2.2 (0.4)	0.32 (0.44)	5.6 (0.4)	154.5 (2.1)
Pe Ell - A	4.1 (0.3)	2.7 (0.7)	0.66 (0.54)	5.4 (0.9)	154.3 (4.8)
Pe Ell - S	3.9 (0.6)	2.0 (0.4)	0.03 (0.14)	5.1 (0.5)	149.4 (7.2)
Wendling - A	4.4 (0.2)	3.4 (0.7)	1.65 (0.65)	6.0 (0.5)	157.2 (7.8)
Wendling - S	4.1 (0.3)	2.2 (0.4)	0.12 (0.25)	5.4 (0.4)	151.3 (6.1)
Forks - A	3.9 (0.5)	2.9 (0.8)	1.01 (0.75)	5.9 (0.6)	159.7 (5.7)
Forks - S	3.8 (0.6)	2.0 (0.4)	0.04 (0.12)	5.4 (0.5)	155.6 (6.3)

1.8-11.0% ($\bar{x}$ = 3.9, SD = 1.9) in Pe Ell, 1.8-8.2% ($\bar{x}$ = 4.8, SD = 1.8) in Wendling, and 0.6-6.2% ($\bar{x}$ = 3.8, SD = 1.5) in Forks. Mean seasonal values for condition indices are given in Table 1.

Survival

We documented 25 mortalities of elk; nine were non-human (three predation, two malnutrition and four due to unknown factors for which human causes were eliminated) and 16 were human-related (three legal harvest, four illegal kills, one wounding loss and eight capture related). An additional three elk were censored. We excluded capture-related mortalities from all analyses. Age of non-human ($\bar{x}$ = 6.9, SE = 1.6, N = 9) and human-related ($\bar{x}$ = 5.4, SE = 1.0, N = 8) mortalities did not differ (t_{15} = 0.8, P = 0.456).

All mortality sources

During June through May survival of adult females varied from 1.00 (SE = 0.00) to 0.74 (SE = 0.08) for all mortality sources inclusive (Table 2). Seasonal survival rates varied from 0.78 to 1.0 for SSA and from 0.82 to 1.0 for survival over winter.

Among populations, annual survival was correlated (r_s = 0.627, P = 0.071) with rBCS measured in spring. SSA survival was correlated with rBCS (r_s = 0.615, P = 0.059) and IFBF (r_s = 0.567, P = 0.088) measured in spring, whereas survival over winter was not correlated with any measure of condition.

Individual logistic models of adult female survival indicated that survival was related to loin muscle thickness (χ^2 = 5.4, P = 0.019) and wBCS (χ^2 = 4.7, P = 0.031) for all mortality sources inclu-

Table 2. Annual (± SE) June-May survival rates including both human and non-human mortality (All), only non-human related mortality (Non-human), and only human-caused mortality (Human) for elk in the Nooksack, Pe Ell and Forks, Washington, and in the Wendling, Oregon, study areas.

Area	Year	All	Non-human	Human	N
Nooksack	2000-2002	1.000 (0)	1.000 (0)	1.000 (0)	18
	2001-2002	0.882 (0.080)	0.938 (0.062)	0.941 (0.061)	18
	2002-2003	1.000 (0)	1.000 (0)	1.000 (0)	14
	$\bar{x}$	0.957 (0.031)	0.978 (0.021)	0.978 (0.021)	
Pe Ell	2001-2002	0.947 (0.051)	0.947 (0.051)	1.000 (0)	22
	2002-2003	0.885 (0.086)	1.000 (0)	0.885 (0.086)	20
	$\bar{x}$	0.916 (0.048)	0.967 (0.032)	0.947 (0.040)	
Forks	2001-2002	0.838 (0.087)	0.882 (0.078)	0.950 (0.055)	20
	2002-2003	0.740 (0.084)	0.856 (0.073)	0.865 (0.071)	16
	$\bar{x}$	0.812 (0.059)	0.889 (0.050)	0.913 (0.045)	
Wendling	2001-2002	0.824 (0.089)	1.000 (0)	0.824 (0.089)	20
	2002-2003	1.000 (0)	1.000 (0)	1.000 (0)	15
	$\bar{x}$	0.906 (0.051)	1.000 (0)	0.906 (0.051)	

sive. The best overall model ($\chi^2 = 8.3$, P = 0.004) of individual elk vulnerability to mortality included only loin muscle thickness and described increased probability of death for individuals as loin muscle depth decreased (β = -1.24 (SE = 0.44), odds ratio = 0.291 (95% CI = 0.123-0.689)); this model successfully classified 62% of female elk mortalities. Odds ratios indicated that likelihood of dying increased approximately 3.4X for each cm less loin muscle. No other variables (i.e. area, season, age, current season's lactation status, lactation status previous season, lactation status two years previous, current season's pregnancy status, pregnancy status the previous year, pregnancy status two years previously, rBCS, maximum subcutaneous fat thickness, girth, IFBF and IFBF the previous season) were related to individual survival probability.

Non-human mortality sources

The June-May survival of adult females varied from 1.00 (SE = 0.00) to 0.86 (SE = 0.07) for non-human mortality sources only (see Table 1). Seasonal survival rates ranged between 0.83 and 1.0 for survival over summer and between 0.96 and 1.0 for survival over winter.

Among populations, annual survival was not correlated with nutritional condition or condition indices. Seasonally, SSA survival was correlated with rBCS ($r_s = 0.615$, P = 0.059) and IFBF ($r_s = 0.567$, P = 0.088). Survival over winter was correlated with wBCS ($r_s = 0.677$, P = 0.045).

For non-human related mortality, individual survival was related to individual logistic models containing season ($\chi^2 = 5.5$, P = 0.019; probability of dying in winter = 0.157 (0.019-1.271) v. SSA), wBCS ($\chi^2 = 8.2$, P = 0.004), rBCS ($\chi^2 = 11.3$, P = 0.001), loin muscle thickness ($\chi^2 = 9.6$, P = 0.002), girth ($\chi^2 = 2.8$, P = 0.095), and IFBF ($\chi^2 = 12.2$, P = 0.001). The best overall model ($\chi^2 = 16.1$, P = 0.0003) of individual elk vulnerability to non-human mortality included both loin muscle thickness ($\chi^2 = 5.7$, P = 0.017) and IFBF ($\chi^2 = 4.9$, P = 0.027) and indicated an inverse relationship between probability of death and loin muscle thickness (β = -1.26 (SE = 0.46); odds ratio = 0.361 (95% CI = 0.156-0.832)) and IFBF (β = -0.35 (SE = 0.16); odds ratio = 0.702 (95% CI = 0.514-0.960)). This model successfully classified 79% of female elk mortalities. Odds ratios indicated that likelihood of dying increased approximately 2.8X for each cm of loin muscle cat-

abolized and 1.4X for each percent less IFBF. No other variables (area, age, current season's lactation status, lactation status previous season, lactation status two years previously, current season's pregnancy status, pregnancy status the previous year, pregnancy status two years previously, maximum subcutaneous fat thickness, and IFBF the previous season) were related to individual survival probability.

Human-caused mortality sources

The June-May survival of adult females varied from 1.00 (SE = 0.00) to 0.82 (SE = 0.08) for human-caused mortality sources only (see Table 1). Seasonal survival rates ranged between 0.94 and 1.0 for survival over summer and between 0.82 and 1.0 for survival over winter.

Among populations, annual survival and overwinter survival were not correlated with nutritional condition or condition indices. Seasonally, SSA survival was correlated with rBCS ($r_s = 0.696$, P = 0.036) and IFBF ($r_s = 0.696$, P = 0.036). No variables (area, age, season, current season's lactation status, lactation status previous season, lactation status two years previously, current season's pregnancy status, pregnancy status the previous year, pregnancy status two years previously, wBCS, rBCS, maximum subcutaneous fat thickness, loin muscle thickness, girth, IFBF or IFBF the previous season) were related to survival probability for individual elk for human-caused mortality sources.

Discussion

Nutritional condition of ungulates results from differences in energy acquisition minus the energy expended for maintenance and other life processes; declines in individual condition are thus primarily due to reductions in the level of nutrition that individuals in a population can attain and store. Poor condition in elk can affect fecundity (Clutton-Brock et al. 1982, Cook et al. 2004, Bender & Cook 2005, Bender et al. in press) and juvenile survival (Cook et al. 2004, Bender et al. 2006). Lactating elk, the most energetically challenged individuals in the population (Cook et al. 2004), achieved body fat levels of 5.9-12.3% in our study areas, levels that were approximately 0.35-0.72 of what lactating elk could accrue on optimum nutrition ($\bar{x}$ = 17; maximum = approximately 22%; Cook et al. 2004). In experimental studies with penned elk, these body fat levels were indicative of marginal (8-12%

body fat) to poor nutrition (< 8% body fat) during summer-early autumn (Cook et al. 2004). These condition levels were shown to influence reproduction and survival through delayed puberty, delayed breeding, enhanced probability of death in harsh winters, and reduced pregnancy, with relatively acute effects occurring at the lower end of this range (Cook et al. 2004). These predicted relations between nutritional condition and fecundity and juvenile survival have been borne out in studies of free ranging elk (Bender & Cook 2005, Bender et al. 2006). In this study, we found that vulnerability to mortality of adult female elk was also affected by nutritional condition even though our observed levels of condition were well above levels associated with starvation mortality ($\leq$ 2% body fat; Cook et al. 2004). This was true for both population-level survival rates and for individual survival probabilities and it supports results of penned elk experiments showing an elevated level of susceptibility to over-winter starvation mortality of female elk with even moderate levels of body fat (8-12%) in autumn under simulated harsh winter conditions (Cook et al. 2004).

Although not mutually exclusive, declines in condition occur in a predictable sequence. Subcutaneous fat is catabolized first, followed by visceral fat, and then marrow fat. At some point in this process, mobilization of muscle mass accelerates to meet both nitrogen and energy requirements (Harris 1945, de Calesta et al. 1975, Parker et al. 1993). Thus, elk depend upon both fat reserves and muscle mass to meet energy and nitrogen requirements for survival and reproduction (Landete-Castillejos et al. 2003); therefore, both may potentially influence survival of adult elk. Because elk and other homeotherms depend primarily upon body fat as energy reserves, we anticipated that fat levels would best predict individual vulnerability to mortality. This was only partially the case, however, for our individual elk logistic analysis.

Survival based on our herd-level evaluation was generally correlated to estimates of IFBF and rBCS, whereas individual vulnerability was related to several measures or indices of nutritional condition, most importantly loin muscle thickness, an index of muscle catabolism. Although most of the indices of condition in our analyses are at least weakly intercorrelated, they do not measure the same attributes of the elk. Subcutaneous fat thickness and, to a lesser extent, rBCS reflect fat levels whereas loin muscle thickness is solely a measure of lean tissue and thus provides an index to levels of protein catabolism. Cook et al. (2001) found that in elk both IFBF and rBCS change approximately linearly as nutritional condition varies. However, thickness of loin muscle does not vary until elk are in relatively poor condition (Mitchell et al. 1976) because catabolism of lean tissue accelerates as nutritional condition declines, most markedly as individuals approach the lowest levels of condition (Torbit et al. 1985, Watkins et al. 1992, Parker et al. 1993). Experimental studies indicate a threshold of about 4.2 cm of loin muscle thickness, below which adult female Rocky Mountain elk have a high probability of dying (Cook et al. 2004).

Thus, measures of body fat may be a better indicator of overall survival rates at the herd level because body fat in general provides an index of overall herd nutritional status (Bender & Cook 2005, Bender et al. 2006), whereas loin muscle thickness does not. For example, there was a 2-fold difference in body fat among our herds, but much smaller differences in loin muscle thickness (see Table 1). Conversely, probability of mortality of individual elk may be better reflected in loin muscle thickness than in body fat, because substantial reductions in loin muscle may better reflect dangerously low levels of endogenous energy reserves than do low levels of body fat (Mitchell et al. 1976).

Because our study populations reflected a range of fat levels from the best documented for free ranging elk (Nooksack) to among the worst (Pe Ell, Forks; Cook et al. 2002, Bender & Cook 2005, Bender et al. 2006), these levels were likely reflective of conditions facing most PNW elk populations. Annual adult female survival among our study populations (0.74-1.00) also spanned the range of survival documented for elk in North America: 0.97 (Ballard et al. 2000) to 0.87 (Unsworth et al. 1993) for unhunted populations and 0.90 (Ballard et al. 2000) to 0.78 (Freddy 1987) for hunted populations. Compared with the highest published levels, mean survival among years within sites (0.78-0.96) in our study populations ranged between 0.76 and 0.99 of maximum potential levels. However, the nutritive value of forage available to elk in our study areas limited development of nutritional condition to 0.35-0.72 of potential. Elk were apparently able to 'buffer' the limiting effects of nutrition, such that effects of limited nutrition on adult survival were less than effects on nutritional condition. This concurs with observations that resource limitation affects condition before fecundity and survival parameters,

with adult survival being the last factor affected, usually only as a population nears ecological carrying capacity (Gaillard et al. 2000, Eberhardt 2002, Bender & Cook 2005).

However, our data also indicate that survival of adult female elk was influenced by levels of condition higher than those associated with extreme nutritional stress (Cook et al. 2004). This suggests that adult female elk may be predisposed to mortality even by moderate nutritional limitations and concomitant fat levels or other condition indices well above those associated with starvation ($\leq$ 2% body fat; Cook et al. 2004). This may occur because elk at moderately low levels of nutrition and condition may be less vigilant, less likely to adequately flee perceived dangers, and may be more susceptible to parasites or disease (Davidson & Doster 1997, Bender & Hall 2004). Assumptions that mortality is additive in adult female elk populations if condition indices are greater than levels associated with starvation mortality may overestimate the impacts of proximate mortality factors in elk population dynamics. For example, Kunkel & Pletscher (1999) assumed that predation was additive for adult female elk when femur marrow fat (FMF) levels were > 35%, and Gula (2004) assumed that red deer were in 'good' condition at FMF = 83%. Although above levels associated with starvation (12% FMF), FMF < 90% in elk indicates body fat levels of < 6% (Cook et al. 2001), the approximate minimum level necessary for oestrous and well below mean fat levels in our study populations in which we saw significant condition-mortality relations, even though mortality was only rarely (two out of 25) directly attributable to starvation. Assumptions that adult female survival is unaffected by nutritional condition at levels higher than at or near starvation may result in overestimation of adult female survival rates in management prescriptions or models, and thus in overestimation of population rates of increase and sustainable harvests.

Management implications

Adult female elk may be predisposed to mortality at condition levels higher than commonly assumed. Assumptions that survival is unaffected by condition as long as condition indices are well above levels associated with starvation mortality are unwarranted and may result in overestimation of impacts of proximate mortality factors in elk population dynamics. Because nutritional condition can affect adult elk survival, adult and juvenile fecundity, and juvenile survival (Cook et al. 2004, Bender & Cook 2005, Bender et al. 2006, our study), managers need to consider these effects when evaluating impacts of proximate mortality factors on elk populations and when modeling elk populations and harvest. This necessitates the collection of data on nutritional condition to predict the possible magnitude of these effects locally for effective management. However, methods used to collect condition data must be valid and correctly interpreted, or conclusions may be erroneous. For example, FMF is often used to assess condition (Bubenik 1982, Kunkel & Pletscher 1999, Gula 2004), but interpretations of FMF levels are often incorrect, i.e. FMF levels of < 90% are often used to indicate satisfactory condition unlikely to affect survival, when in fact elk are in reduced condition that may predispose them to mortality when FMF $\leq$ 90% ($\leq$ 6% body fat; Cook et al. 2001).

Nutritional condition affected adult survival, adult fecundity (Trainer 1971, Bender et al. 2006), and juvenile fecundity (Bender et al. 2006) in the PNW. Because nutritional condition is a consequence of a suite of habitat influences (Hanks 1981, Clutton-Brock et al. 1982, Verme & Ullrey 1984), extant habitat conditions are limiting elk population performance in the PNW. From our data, we cannot conclude with certainty that nutritional limitations are responsible for elk declines in the PNW, but our data at least indicate that demographic vigour is reduced via nutritional effects, and thus potential rates-of-increase are lessened because of nutritional limitations. Habitat and population management strategies designed to reverse long-term declining trends in elk productivity and populations in the PNW need to be rigorously evaluated with respect to their impacts on elk nutritional condition. Unless management practices can be shown to enhance condition, significant effort and resources may be expended without any positive and predictable response in elk populations.

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References

Adams, L.G., Singer, J.& Dale, B.W. 1995: Caribou calf mortality in Denali National Park, Alaska. - Journal of Wildlife Management 59: 584-594.

Adrian, W.J. 1996: Wildlife forensic field manual. - Association of Midwest Fish and Game Law Enforcement Officers, Denver, Colorado, USA, 211 pp.

Ballard, W.B., Whitlow, H.A., Wakeling, B.F., Brown, R.L., deVos, J.C., Jr. & Wallace, M.C. 2000: Survival of female elk in northern Arizona. - Journal of Wildlife Management 64: 500-504.

Bender, L.C. 2002: Effects of bull elk demographics on age categories of harem bulls. - Wildlife Society Bulletin 30: 193-199.

Bender, L.C., Carlson, E., Schmitt, S.M. & Haufler, J.B. 2002a: Production and survival of elk (Cervus elaphus) calves in Michigan. - American Midland Naturalist 148: 163-171.

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

Bender, L.C., Davison, M.A., Cook, J.G., Cook, R.C. & Hall, P.B. 2006: Assessing elk population status and potential performance in the Nooksack herd area, Washington. - Northwestern Naturalist 87: 98-106.

Bender, L.C., Fowler, P.E., Bernatowitz, J.A., Musser, J.L. & Stream, L.E. 2002b: Effects of open-entry spike bull, limited-entry branched-bull harvesting on elk composition in Washington. - Wildlife Society Bulletin 30: 1078-1084.

Bender, L.C. & Hall, P.B. 2004: Winter fawn survival in black-tailed deer populations affected by hair loss syndrome. - Journal of Wildlife Diseases 40: 444-451.

Bender, L.C., Schirato, G.A., Spencer, R.D., McAllister, K.R. & Murphie, B.L. 2004: Survival, cause-specific mortality, and harvesting of male black-tailed deer in Washington. - Journal of Wildlife Management 68: 868-876.

Bingham, C.M., Wilson, P.R. & Davies, A.S. 1990: Real-time ultrasonography for pregnancy diagnosis and estimation of fetal age in farmed red deer. - Veterinary Record 125: 102.

Bubenik, A.B. 1982: Physiology. - In: Thomas, J.W. & Toweill, D.E. (Eds); Elk of North America: ecology and management. Stackpole Books, Harrisburg, Pennsylvania, USA, pp. 125-179.

Clutton-Brock, T.H., Guinness, F.E. & Albon, S.D. 1982: Red deer: Behavior and ecology of two sexes. - University of Chicago Press, Chicago, Illinois, USA, 378 pp.

Cook, J.G., Cook, R.C., Bender, L.C., Hall, P.B. & Irwin, L.L. 2002: Nutritional influences on Northwestern elk herds: Wild elk capture and nutritional condition assessment. - Progress report, National Council for Air and Stream Improvement, LaGrande, Oregon, USA, 17 pp.

Cook, J.G., Johnson, B.K., Cook, R.C., Delcurto, T., Riggs, R.A., Bryant, L.D. & Irwin, L.L. 2004: Summer-autumn nutrition and birth date influences on reproduction and survival of elk. - Wildlife Monographs 155: 1-61.

Cook, J.G., Quinlan, L.J., Irwin, L.L., Bryant, L.R., Riggs, R.A. & Thomas, J.W. 1996: Nutrition-growth relations of elk calves during late summer and fall. - Journal of Wildlife Management 60: 528-541.

Cook, R.C. 2000: Studies of body condition and reproductive physiology in Rocky Mountain elk. - Master's thesis, University of Idaho, Moscow, Idaho, USA, 117 pp.

Cook, R.C., Cook, J.G., Murray, D.L., Zager, P., Johnson, B.K. & Gratson, M.W. 2001: Development of predictive models of nutritional condition for Rocky Mountain elk. - Journal of Wildlife Management 65: 973-987.

Davidson, W.R. & Doster, G.L. 1997: Health characteristics and white-tailed deer density in the southeastern United States. - In: Mcshea, W.J., Underwood, H.B. & Rappole, J.H. (Eds); The science of overabundance: deer ecology and population management. Smithsonian Institution, Washington D.C., USA, pp. 164-184.

de Calesta, D.S., Nagy, J.G. & Bailey, J.A. 1975: Starving and refeeding mule deer. - Journal of Wildlife Management 39: 663-669.

Depperschmidt, J.D., Torbit, S.C., Alldredge, A.W. & Deblinger, R.D. 1987: Body condition indices for starved pronghorn. - Journal of Wildlife Management 51: 675-678.

Eberhardt, L.L. 2002: A paradigm for population analysis of long-lived vertebrates. - Ecology 83: 2841-2854.

Franklin, J.F. & Dyrness, C.T. 1973: Natural vegetation of Oregon and Washington. - United States Forest Service General Technical Report PNW-8, U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, Oregon, USA, 417 pp.

Freddy, D.L. 1987: The White River elk herd: a perspective, 1960-1985. - Technical Publication Number 37, Colorado Division of Wildlife, Fort Collins, Colorado, USA, 64 pp.

Gaillard, J-M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A. & Toigo, C. 2000: Temporal variation in fitness components and population dynamics of

large herbivores. - Annual Review of Ecology and Systematics 31: 367-393.

Gula, R. 2004: Influence of snow cover on wolf Canis lupus predation patterns in Biesczzady Mountains, Poland. - Wildlife Biology 10: 17-23.

Hamlin, K.L., Pac, D.F., Sime, C.A., Desimone, R.M. & Dusek, G.L. 2000: Evaluating the accuracy of ages obtained by two methods for montane ungulates. - Journal of Wildlife Management 64: 441-449.

Hanks, J. 1981: Characterization of population condition. - In: Fowler, C.W. & Smith, T.D. (Eds.); Dynamics of large mammal populations. John Wiley and Sons, New York, New York, USA, pp. 47-73.

Harris, D. 1945: Symptoms of malnutrition in deer. - Journal of Wildlife Management 9: 319-322.

Hosmer, D.W. & Lemeshow, S. 1989: Applied logistic regression. - John Wiley and Sons, New York, New York, USA, 307 pp.

Huggard, D.J. 1993: Prey selectivity of wolves in Banff National Park. II. Age, sex, and condition of elk. - Canadian Journal of Zoology 71: 140-147.

Keech, M.A., Bowyer, R.T., Ver Hoef, J.M., Boertje, R.D., Dale, B.W. & Stephenson, T.R. 2000: Life-history consequences of maternal condition in Alaskan moose. - Journal of Wildlife Management 64: 450-462.

Küchler, A.W. 1964: Manual to accompany the map, potential natural vegetation of the conterminous United States. - American Geographic Society Special Publication 36, 152 pp.

Kunkel, K. & Pletscher, D.H. 1999: Species-specific population dynamics of cervids in a multipredator ecosystem. - Journal of Wildlife Management 63: 1082-1093.

Landete-Castillejos, T., García, A., Gómez, J.A. & Gallego, L. 2003: Lactation under food constraints in Iberian red deer Cervus elaphus hispanicus. - Wildlife Biology 9: 131-139.

Mitchell, B., McCowan, D. & Nicholson, I.A. 1976: Annual cycles of body weight and condition in Scottish red deer, Cervus elaphus. - Journal of Zoology (London) 180: 107-127.

National Research Council 1985: Nutrient requirements of sheep. 6th revised edition. - National Academy Press, Washington D.C., USA, 99 pp.

National Research Council 1996: Nutrient requirements of beef cattle. 7th revised edition. - National Academy Press, Washington D.C., USA, 232 pp.

Noyes, J.H., Johnson, B.K., Dick, B.L. & Kie, J.G. 2002: Effects of male age and female nutritional condition on elk reproduction. - Journal of Wildlife Management 66: 1301-1307.

Parker, K.L., Gillingham, M.P., Hanley, T.A. & Robbins, C.T. 1993: Seasonal patterns in body mass, body composition, and water transfer rates of free-ranging and captive black-tailed deer (Odocoileus hemionus sitkensis) in Alaska. - Canadian Journal of Zoology 71: 1397-1404.

Pollock, K.H., Winterstein, S.R., Bunck, C.M. & Curtis, P.D. 1989: Survival analysis in telemetry studies: The staggered entry design. - Journal of Wildlife Management 53: 7-15.

Ratcliffe, P.R. 1980: Bone marrow fat as an indicator of condition in Roe Deer. - Acta Theriologica 25, 26: 333-340.

Roy, L.D. & Dorrance, M.J. 1976: Methods of investigating predation of domestic livestock. - Alberta Agriculture, Edmonton, Alberta, Canada, 116 pp.

Sams, M.G., Lochmiller, R.L., Qualls, C.W., Jr., Leslie, D.M., Jr. & Payton, M.E. 1996: Physiological correlates of neonatal mortality in an overpopulated herd of white-tailed deer. - Journal of Mammalogy 77: 179-190.

Torbit, S.C., Carpenter, L.H., Swift, D.M. & Alldredge, A.W. 1985: Differential loss of fat and protein by mule deer during winter. - Journal of Wildlife Management 49: 80-85.

Trainer, C.E. 1971: The relationship of physical condition and fertility of female Roosevelt elk (Cervus canadensis roosevelti) in Oregon. - Master's thesis, Oregon State University, Corvallis, Oregon, USA, 93 pp.

Unsworth, J.W., Kuck, L., Scott, M.D. & Garton, E.O. 1993: Elk mortality in the Clearwater drainage of northcentral Idaho. - Journal of Wildlife Management 57: 495-502.

Verme, L.J. & Ullrey, D.E. 1984: Physiology and nutrition. - In: Halls, L.K. (Ed.); White-tailed deer: Ecology and management. - Stackpole Books, Harrisburg, Pennsylvania, USA, pp. 91-118.

Washington Department of Fish and Wildlife 1997: Washington State management plan for elk. - Wildlife Management Program, Washington Department of Fish and Wildlife, Olympia, Washington, USA, 103 pp.

Watkins, B.E., Witham, J.H. & Ullrey, D.E. 1992: Body composition changes in white-tailed deer fawns during winter. - Canadian Journal of Zoology 70: 1409-1416.

White, G.C., Freddy, D.J., Gill, R.B. & Ellenberger, J.H. 2001: Effect of adult sex ratio on mule deer and elk productivity in Colorado. - Journal of Wildlife Management 65: 543-551.

Whitten, K.R., Garner, G.W., Mauer, F.J. & Harris, R.B. 1992: Productivity and early calf survival in the porcupine caribou herd. - Journal of Wildlife Management 56: 201-212.

Zar, J.H. 1996: Biostatistical analysis. - Prentice Hall, Upper Saddle River, New Jersey, USA, 662 pp.