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Source: Journal of Mammalogy, 94(1):162-172. 2013.
Published By: American Society of Mammalogists
DOI: http://dx.doi.org/10.1644/12-MAMM-A-074.1
URL: http://www.bioone.org/doi/full/10.1644/12-MAMM-A-074.1

Journal of Mammalogy, 94(1):162–172, 2013

Life-history strategies of North American elk: trade-offs associated with reproduction and survival

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The principle of energy allocation states that individuals should attempt to maximize fitness by allocating resources optimally among growth, maintenance, and reproduction. Such allocation may result in trade-offs between survival and reproduction, or between current and future reproduction. We used a marked population of North American elk (*Cervus elaphus*) to determine how energetic costs of reproduction in the current year affect survival and reproduction in the subsequent year. Using a multistate mark–recapture model we examined the influence of individual and environmental variation on trade-offs between these 2 life-history traits. We observed no difference in survival probabilities between pregnant and nonpregnant individuals or as a function of recruiting an offspring. Nonetheless, there was a negative effect of recruiting an offspring in the current year on becoming pregnant the following year. Increased body condition, and higher precipitation, contributed to greater probabilities of becoming pregnant in a particular year regardless of reproductive state and previous recruitment. Costs associated with reproduction led to a reduced probability of future reproduction rather than a reduction in survival. These findings are consistent with risk-sensitive reproductive allocation, where adult survival is maintained through variation in reproductive effort resulting in high and stable adult survival and more-variable reproduction.

Key words: *Cervus elaphus*, fitness, life-history strategy, multistate mark–recapture technique, recruitment, reproductive costs, resource allocation, risk-sensitivity, transition probability, ungulates

DOI: 10.1644/12-MAMM-A-074.1

The principle of energy allocation suggests that energy and time are limited; therefore, individuals should allocate resources optimally among growth, cell maintenance, and reproduction to maximize fitness (Williams 1966). This optimal allocation of energy among various life-history traits often results in trade-offs (Clutton-Brock et al. 1983; Le Bohec et al. 2007; van Noordwijk and de Jong 1986). Two traits thought to be most competitive for limited resources are survival and reproduction (Bardsen et al. 2010; Stearns 1992; Tavecchia et al. 2005). Trade-offs between survival and reproduction have shaped the life-history strategies of many species and are especially apparent among long-lived species (van Noordwijk and de Jong 1986). Long-lived, iteroparous species have evolved strategies for energy allocation to maximize reproductive success over their lifetime by placing greater emphasis on adult survival and less emphasis on any single reproductive event (Drent and Daan 1980; Gaillard and Yoccoz 2003; Hadley et al. 2007). This pattern is especially evident for species living in stochastic environments; individuals may adopt risk-sensitive reproductive allocation where investment in reproduction varies among years to increase survival (Bardsen et al. 2008; Festa-Bianchet and Jorgenson 1998) and allows for greater accumulation of energy to allocate to future attempts at reproduction during more favorable conditions (Bardsen et al. 2011; Stearns 1992). As a result, survival is less variable over a range of conditions, due to environmental canalization of that trait, leaving reproduction to be more variable (Gaillard and Yoccoz 2003; Hamel et al. 2010).

Many studies have attempted to identify trade-offs among life-history traits with variable success, sometimes identifying positive relationships where negative ones were expected (Cam et al. 1998; Toigo et al. 2002; Weladji et al. 2008). Heterogeneity among individuals (Cam et al. 1998), density-dependent feedbacks among populations (Kie et al. 2003; Lomnicki 1978), and environmental stochasticity can mask relationships among life-history traits, making trade-offs difficult to identify (Coulson et al. 2001). Individual variation in age, physical condition, and previous reproductive effort influences pregnancy rates in ungulate populations, and has the potential to interact with various life-history traits (Clutton-Brock et al. 1983; Gerhart et al. 1997; Moyes et al. 2011; Stewart et al. 2005). Moreover, environmental variation can influence availability of resources (Clutton-Brock and Coulson 2002; McCullough 1979), which in turn affects body condition and available energy to invest in reproduction and maintenance (Kie et al. 2003; McCullough 1999; Stewart et al. 2005).

Reproduction in large mammals is energetically demanding, and resource requirements during late gestation and lactation are extremely high (Barboza et al. 2009; Clutton-Brock et al. 1989); as a result intermittent breeding is common (Clutton-Brock and Coulson 2002; Festa-Bianchet and Côté 2008; Gerhart et al. 1997; Hamel et al. 2009). North American elk (*Cervus elaphus*) along with other long-lived species exhibit risk-sensitive reproductive allocation where reproductive success over their lifetime is maximized through maintenance of high and stable adult survival and variable reproductive output (Gaillard and Yoccoz 2003; Hamel et al. 2010). In elk, the number of offspring typically is fixed within the species at a maximum of 1 per year; however, age at maturity and timing of reproductive pauses may vary within the population (Clutton-Brock 1982; Stewart et al. 2005).

Effects of age structure have been documented in elk (Clutton-Brock et al. 1983; Stewart et al. 2005), with increased pregnancy rates for prime-age individuals (Nussey et al. 2009). This relationship likely results from greater allocation of resources to reproduction instead of growth, although dominance and experience also contribute to a greater likelihood of reproductive success (Hamel et al. 2009). Such individual variation needs to be assessed when attempting to quantify the energetic costs of reproduction and resulting trade-offs among life-history characteristics. Particular individuals may have phenotypic advantages such as larger body size, the ability to assimilate nutrients more efficiently, or higher dominance status, resulting in access to more or better-quality resources (Clutton-Brock et al. 1983; Green 1990; Moyes et al. 2011).

North American elk are classified as capital breeders relying on body reserves obtained during summer for reproduction and overwinter survival (Festa-Bianchet et al. 1998; Moyes et al. 2006; Toigo et al. 2002). Elk also rely heavily on additional resources during birth and rearing periods (spring, summer, and fall) to provision offspring (Parker et al. 2009). As interspecific competition for resources increases, physical condition, pregnancy rates, and recruitment decrease (Clutton-Brock and Coulson 2002; Kie et al. 2003; McCullough 1979, 1999; Stewart et al. 2005). As a result there may be a threshold level of fat or energy stores, above which adequate energy can be allocated to both survival and reproduction with little trade-off (Doughty and Shine 1997).

In semiarid environments, annual fluctuations in availability of summer forage are driven by changes in winter or spring precipitation and can greatly influence energy available to reproduction and survival (Bardsen and Tveraa 2012; Derner et al. 2008; Mautz 1978). In years when summer resources are high, a greater proportion of individuals within the population may experience improved foraging opportunities enabling them to replenish energy stores and overcome costs associated with recruiting an offspring (Gerhart et al. 1997; Parker et al. 2009; Tollefson et al. 2010). Such opportunities allow greater allocation of resources to future survival and reproduction (Lomnicki 1978; Mautz 1978; Tavecchia et al. 2005; Toigo et al. 2002; White et al. 1997). As a result individuals reproduce with few negative costs. Conversely, in years when forage is limited, trade-offs may become more apparent. We also may expect to see greater variation in individual performance (Lomnicki 1978; Toigo et al. 2002), because intraspecific competition may intensify any variation in dominance status, age, or experience.

Given the principle of energy allocation and high energy demands associated with reproduction, we expect that in populations of large mammals where intraspecific competition for resources is strong, there will be trade-offs among life-history traits. We used data from an intensively studied population of elk to examine costs associated with reproduction and to identify trade-offs among life-history characteristics such as current reproduction, survival, and future reproduction. We hypothesized that trade-offs among life-history traits would be exhibited by differences in nutrition obtained during spring, summer, and autumn, while experimentally holding the effects of winter constant. We predicted a variable response in reproductive output by elk based on summer resource availability in which trade-offs among reproduction and survival, or current and future reproduction, occur. We predicted that individuals follow a life-history strategy where adult survival is maximized, and any cost of reproduction is realized as a lower probability of reproducing the following year. We further predicted a greater cost of reproduction when resources were most limited. Finally, we predicted that survival does not vary among reproductive states and expected more annual variability in reproduction than in survival (sensu Gaillard et al. 2000).

Materials and Methods

Study area and population.—We conducted an analysis of a capture–recapture data set for a population of North American elk inhabiting Starkey Experimental Forest and Range (hereafter Starkey), in the Blue Mountains of northeastern Oregon, 35 km southwest of La Grande, Oregon (45°12′N, 118°3′W—Rowland et al. 1997; Stewart et al. 2005). Starkey encompasses 10,125 ha of public land managed by the United

States Forest Service. The Starkey Project was originally designed to measure the response of mule deer (*Odocoileus hemionus*) and elk to various forest and range management scenarios, including logging, grazing, recreation, and other manipulative experiments (Rowland et al. 1997). As a result, the study area represents similar land-use patterns as the surrounding forest landscape and is representative of inland national forests throughout the intermountain west. Hunting occurs on Starkey and a few females were harvested each year; those harvested individuals were censored from further analyses.

Starkey is surrounded by a 2.4-m-tall fence that prevents immigration or emigration of elk, thereby creating a closed population (Rowland et al. 1997; Stewart et al. 2002). The landscape is representative of summer habitat in this region. Elk on Starkey cannot migrate to traditional winter range. The elk have been concentrated on a low-elevation wintering ground within the study area from December through April or May, where they are fed a maintenance diet of alfalfa hay (*Medicago sativa*—Davidson et al. 2012; Rowland et al. 1997; Stewart et al. 2005, 2006). Use of the wintering area depends largely on snow conditions.

Elk enter the wintering grounds from mid-December to late-January. As part of the Starkey Project protocol, upon entering the wintering ground, elk are baited into a capture pasture and then moved through a system of alleyways to the handling facility (Stewart et al. 2005, 2006). Individual elk are identified by uniquely numbered ear tags. Individuals captured initially as young or yearlings are recorded as known-age individuals, and those captured as adults are recorded as an adult age class (Stewart et al. 2005). For this analysis we only included known-age individuals that were $\geq$1 year old. Most female elk reach maturity at 2 years in moderate to high population densities and are considered prime-aged between 4 and 9 years (Nussey et al. 2009). At extremely low population densities yearlings can become pregnant; however, this event is uncommon (Stewart et al. 2005). This population has been monitored since 1989; thus most individuals are currently of known age (Rowland et al. 1997). Our analysis only includes information from 2001 to 2005, because that was the time when information on body condition and pregnancy was the most complete, as well as a time period when effects from other manipulative studies were minimal. During this period the population was maintained at moderate densities, ranging from 4.8 to 8.7 elk/km^2; those densities have been reported to be moderate relative to ecological carrying capacity on Starkey (Davidson et al. 2012; Rowland et al. 1997; Stewart et al. 2005).

Data collection.—To identify trade-offs among life-history traits and to account for differential costs, we assessed cost of reproduction in 2 ways; 1st, whether an individual was pregnant in a particular year (i.e., reproductive state), and 2nd, whether females were lactating at time of capture. Blood was drawn from the jugular vein for adult and yearling females, and pregnancy was measured by presence of pregnancy-specific protein B (Keech et al. 2000; Noyes et al. 1997; Stewart et al. 2005). If animals were lactating at time of capture they were recorded as having reared an offspring through summer (Stewart et al. 2005). This estimate is conservative, because some individuals may have completed lactation by time of capture.

The age of an individual was identified at time of 1st capture. Age was recorded as a continuous, time-varying covariate. We also explored the potential for a nonlinear effect of age on survival and reproduction. Age class (yearling or adult) also was identified and included as a binomial covariate. We assessed body condition at time of capture. This measure accounted for yearly variation in resource acquisition that could determine the amount of energy available to allocate among life-history traits (Parker et al. 2009). We measured depth of maximum rump fat (max fat) using ultrasonography, to provide an annual index of body condition for each individual female (Keech et al. 2000; Stephenson et al. 1998). All aspects of this research were approved by the Institutional Animal Care and Use Committees at the University of Alaska Fairbanks (IACUC 01–34) and the United States Forest Service Starkey Project, and they were in keeping with protocols adopted by the American Society of Mammalogists for field research involving mammals (Sikes et al. 2011).

To examine how annual fluctuations in resource availability influence costs associated with reproduction and resulting trade-offs, we used 2 measures of habitat productivity: seasonal precipitation and an index of group max fat. We used seasonal precipitation as a correlate for plant productivity (Derner et al. 2008). We obtained seasonal data on precipitation from the National Atmospheric Deposition Program weather station located on Starkey (Stewart et al. 2002). Precipitation was classified as winter (November–March) and summer (July–September) to approximate seasons defined by Stewart et al. (2002) and correspond with the time when costs of gestation and lactation are greatest. In semiarid environments, winter and spring precipitation provides a strong index to summer plant growth (Derner et al. 2008). Moreover, we held the effects of winter constant through maintenance feeding and thus considered winter precipitation to reflect resource availability during spring and summer. An average group max fat value was calculated from all the individuals captured in a given year and used as an index of resource availability for the population (Tollefson et al. 2010).

Analyses.—To identify cost of reproduction and trade-offs between reproduction and survival, or current and future reproduction, we analyzed data using a multistate, mark–recapture model in program MARK (White and Burnham 1999). This method allowed us to simultaneously estimate survival (Φ), recapture probabilities (p), and probabilities of transitioning between reproductive states (ψ; pregnant or not pregnant—Brownie et al. 1993; Nichols et al. 1994). At time of capture, the reproductive state of an individual was identified as either pregnant or not pregnant. At this time we also recorded the following individual covariates, and incorporated them into the analysis: lactation status as an indication of

recruitment (Stewart et al. 2005), age, and body condition. Capture histories from 482 individuals were used in the models to generate parameter estimates (Φ, p, and ψ) for each reproductive state (Brownie et al. 1993; Nichols and Kendall 1995). Individual covariates were converted to standard normal values ($\mu = 0$, $SD \geq 1$) to allow for direct comparison of covariate effects (β). Missing values were rare and were replaced with the mean ($\mu = 0$) for the population. Replacing missing values with the population mean ($\mu = 0$) can lead to slightly conservative estimates of covariate effects (White and Burnham 1999). MARK, however, cannot process missing values, making the substitution necessary to allow that capture occasion to contribute to the estimation of other model parameters (White and Burnham 1999). Individual and environmental covariates were then included in models to test hypotheses regarding their influence on life-history traits.

We implemented model selection in a multistep process whereby alternative model structures were explored for each parameter of interest (Φ, p, and ψ), while keeping the structure for the other parameters constant (Glenn et al. 2011; Lescroel et al. 2009). In each instance, we began with the most general model structure allowing the parameter estimates to vary for group and age by time; we then decreased complexity until we achieved convergence. We then retained the best model structure for a given parameter (e.g., p) while modeling the next parameter of interest (e.g., Φ and ψ—Arnold 2010). We 1st constrained models of recapture probability, then transition probability, and finally survival probabilities to identify the best basic model structure. We then introduced covariates into this model to test our a priori hypotheses about life-history trade-offs and the influence of individual and environmental variation (Hamel et al. 2009; Moyes et al. 2009; Weladji et al. 2008). Age was included in the basic model set because other studies have identified age structure as an important determinant of resource allocation, especially in large mammals (Clutton-Brock et al. 1983; Moyes et al. 2011; Stewart et al. 2005).

To assess the influence of individual and environmental variation on trade-offs between survival, current reproduction, and future reproduction, group covariates related to winter precipitation, summer precipitation, average group max fat, reproductive state (pregnant or not pregnant), age, age class (yearling or adult), lactation status, max fat, and year were incorporated into models of survival (Φ) and transition (ψ). We also were interested in potential nonlinear or threshold effects of age and max fat on reproduction. We also revisited our model set after identifying the best models containing covariates, and explored more-complex model structures to be certain that important relationships were not overlooked. Indeed, incorporation of covariates in 1 portion of the model (e.g., recapture) can influence relationships in the other, such as survival or transition.

In this population, recapture rates are high because individuals cannot migrate outside Starkey. Because movement onto the wintering area and subsequent capture is variable and encouraged through baiting with alfalfa, we were concerned that resource availability during summer or winter could influence winter attendance on the feeding grounds, or that the amount of winter precipitation would influence capture probabilities. We also were interested if reproductive state, individual body condition, or lactation status would influence capture probabilities. To test these hypotheses we included covariates for winter precipitation, body condition (max fat and group max fat), reproductive states, and age class when modeling recapture probabilities.

Support for each model was assessed using Akaike information criterion corrected for both overdispersion and small sample size ($QAIC_c$—Burnham and Anderson 2002). We used model averaging to generate parameter estimates for models with a $\Delta QAIC_c$ weight of >0.05 (Arnold 2010; Burnham and Anderson 2002). Parameter estimates generated by model averaging are more robust than estimates from the best model, because they reduce model selection bias and incorporate model uncertainty (Johnson and Omland 2004).

Program U-CARE (Choquet et al. 2009) was used to assess goodness-of-fit for the most general model, which allowed survival and transition to vary by state and time. This procedure identified the extent of heterogeneity within data and adjusts the model-selection process and parameter estimates to account for this bias, resulting in more conservative estimates. We adjusted AIC values based on $\hat{c}$ ($\hat{c} = \chi^2/d.f.$—Lebreton et al. 1992), to obtain quasi-Akaike information criterion (QAIC) values that accounted for this heterogeneity or overdispersion in data (Burnham and Anderson 2002). We ran a Spearman-rank correlation on the covariates to determine the extent of collinearity. The covariates were not highly correlated; correlation coefficients fell between –0.41 (max fat and lactation) and 0.23 (lactation and age).

Estimates of covariate effects were generated using the logit-link function in program MARK. This function calculates estimates using the logit scale, which constrains probabilities to fall between 0 and 1. We used the logit-link function to back-transform the β estimates and determine the true covariate effects. This function can cause the appearance of nonlinear relationships when displayed on the probability scale as estimates reach the bounds of 0 or 1 (Zar 2010).

Results

Between the winter of 2001–2002 and the winter of 2005–2006, we captured 482 uniquely identified female elk (Table 1). All individuals were known age; their reproductive state and body condition were determined annually at time of capture. The goodness-of-fit test identified slight overdispersion in the data ($\chi^2_{27} = 32.9$, $\hat{c} = 1.18$) for the general state (s) by time (t) model, Φ(s*t) p(s*t) ψ(s*t). We adjusted AIC_c scores accordingly to produce $QAIC_c$ values (Lebreton et al. 1992).

The best-supported model for captures contained an additive effect of age class and group max fat (GMF; p[age class + GMF]). Capture probabilities were negatively influenced by

Table 1.—Sample size of adult and yearling female elk (*Cervus elaphus*) captured on the wintering grounds (December–February), for each capture occasion, on the Starkey Experimental Forest and Range, Oregon.

Year	Age class	*n*
2001–2002	Adult	249
	Yearling	50
2002–2003	Adult	168
	Yearling	24
2003–2004	Adult	171
	Yearling	28
2004–2005	Adult	118
	Yearling	12
2005–2006	Adult	142
	Yearling	28

group max fat ($\beta = -0.74$, $SE = 0.15$) and age class, yearling or adult ($\beta = -2.58$, $SE = 0.55$), with yearlings exhibiting lower capture probabilities. Capture probabilities varied annually based on group max fat, but averaged 33% ($SE = 0.11\%$) for yearlings, and 82% ($SE = 0.02\%$) for adults. There was no support for differential capture probabilities associated with reproductive state or age. Average group max fat was a better predictor of capture probabilities than winter precipitation or annual variation alone. We retained this best model of capture probability when modeling survival and transition probabilities.

Survival analysis.—Survival probabilities were consistently high and influenced by age (Fig. 1). Summer and winter precipitation occurred in the top models (Table 2); however, the small effect size and imprecise parameter estimates indicate that summer precipitation had only a weak effect on survival (Table 3). Models containing the covariates for reproductive output, reproductive state, or lactation had a $\Delta QAIC_c > 2$, indicating little support for these models. Model-averaged parameter estimates confirm a lack of importance for these covariates, with a small effect size, and 95% confidence intervals (95% *CI*s) overlapping 0 (Table 3). There was a negative linear effect of age on survival, indicating the potential for a senescent decline in survival for this population (Fig. 1).

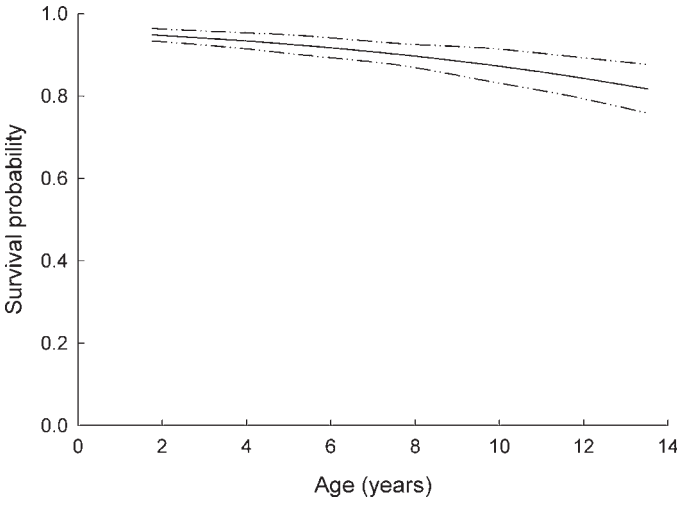

Fig. 1.—Model averaged estimates (± *SE*; Table 2) of female survival by age for adult elk (*Cervus elaphus*) on the Starkey Experimental Forest and Range, La Grande, Oregon, 2001–2005. The covariate β was back-transformed using the logit-link function to generate effect plots.

Transition analysis.—Transition probability was modeled as the probability of an individual becoming pregnant the following year. There was no support for differential transition probabilities based on reproductive state (pregnant or not pregnant). The best model structure prior to the inclusion of individual covariates contained a quadratic effect of age, and an additive effect of winter precipitation on transition (model 22: $\Delta QAIC_c = 79.7$; Table 2); however, the inclusion of individual covariates greatly improved model performance. The most-parsimonious model identified a quadratic effect of age^2 and max fat^2, and an additive effect of lactation and winter precipitation on transition probabilities ($\Delta QAIC_c = 0$; Table 2). Removal of any 1 individual covariate resulted in a decrease in model support between 14 and 18 $\Delta QAIC_c$ units. There were multiple competitive models within our model set; thus we used model averaging to generate robust parameter estimates and identify which covariates influenced transition probabilities (Table 3).

Previous reproductive effort.—Reproductive state (pregnant or not pregnant) was included in our suite of top models; however, there was little support for this variable, with a $\Delta QAIC_c$ weight of 0.11. The model-averaged β further confirmed this lack of support because the effect size was small and contained 0 within the 95% *CI*s (Table 3). A negative effect of lactation on transition to pregnant was identified in all the top models, indicating strong support for this relationship (Tables 2 and 3). Parameter estimates indicate a 17% decrease in the probability of transitioning to pregnant if an individual was lactating ($\psi_{nonlact} = 0.92$, 95% $CI = 0.87$–0.97; $\psi_{lact} = 0.73$, 95% $CI = 0.60$–0.85). There was little support for an interaction between pregnancy status and lactation, or lactation and max fat, on transition to breeding; estimates of 95% *CI*s broadly overlapped 0 for those interactions (Table 3). The lack of support for these interactions indicates a primarily additive effect of lactation on transition to pregnancy.

Environmental variation.—Transition probabilities varied among years in relation to winter precipitation, indicating that the population was sensitive to environmental fluctuation and changes in resource availability. Probability of transitioning to pregnant increased with increasing winter precipitation (Fig. 2A). Removing winter precipitation from the model and including only individual covariates greatly reduced model performance (model 21; $\Delta QAIC_c = 40.2$; Table 2). There was no support for an interaction between lactation and winter precipitation, indicating that the effect of winter precipitation was similar for lactating versus nonlactating individuals. The steep slope of the covariate effect indicates that transition probability was sensitive to even small increases in winter

TABLE 2.—Results from multistate model for survival (Φ) and transition (ψ) probabilities according to age and reproductive state of North American elk (*Cervus elaphus*) on the Starkey Experimental Forest and Range, La Grande, Oregon, 2001–2005. Models were created using a constant structure on recaptures (*p*[age class + GMF], where GMF is group max fat), and were evaluated using Akaike information criterion corrected for both overdispersion and small sample size ($QAIC_c$). Models with a $QAIC_c$ weight ≥ 0.5 were used to generate model-averaged parameter estimates. Probability of transitioning to pregnant refers to the probability that an individual will become pregnant the following year given the influence of model parameters. Reproductive output was identified by whether an individual was pregnant or lactating in the current year. Lactation was used as an index of recruitment. Age class groups individuals into 2 classes (yearlings or adults); age is a continuous time-varying covariate; winter precip refers to winter–spring precipitation (November–March); and summer precip refers to summer precipitation (July–September). Precipitation is included as an index to summer resource availability. The influence of female condition was measured through depth of maximum rump fat (max fat). The squared term on a parameter represents both a linear and quadratic term in the model. Y = yes.

No.[a]	Model parameters	$\Delta QAIC_c$[b]	w_i[c]	K[d]	Qdev[e]	Used in model averaging
Modeling survival probabilities (Φ)						
1	Age + winter precip	0.00	0.33	13	1,104	Y
2	Age + summer precip	0.99	0.20	13	1,105	Y
3	Age	1.45	0.16	12	1,108	Y
5	Age + age^2	2.74	0.08	13	1,107	Y
7	Age + pregnant	3.13	0.07	13	1,107	Y
8	Age + lactating	3.16	0.07	13	1,107	Y
11	Age + max fat	3.53	0.06	13	1,108	Y
12	Age + pregnant + lactating	4.67	0.03	14	1,107	
15	Winter precipitation	8.44	0.00	12	1,115	
16	Null	10.23	0.00	11	1,118	
17	Age class	12.06	0.00	12	1,118	
18	Year	12.33	0.00	14	1,114	
19	Age class*pregnant	13.23	0.00	13	1,117	
Modeling probability of transitioning to pregnant (ψ)						
3	Age^2 + max fat^2 + lactating + winter precip	0.00	0.30	12	1,108	Y
4	Age^2 + max fat^2 + lactating + winter precip + summer precip	0.28	0.26	13	1,106	Y
6	Age^2 + max fat*lactating + winter precip	1.58	0.14	12	1,109	Y
9	Age^2 + max fat + lactating + winter precip	1.83	0.12	11	1,111	Y
10	Age^2 + max fat^2 + lactating + winter precip + pregnant	1.98	0.11	13	1,107	Y
13	Age^2 + max fat^2 + winter precip + pregnant*lactating	3.73	0.05	14	1,107	Y
14	Age^2 + max fat^2 + winter precip*lactating	6.03	0.01	13	1,112	
20	Max fat^2 + lactating + winter precip + age class*pregnant	13.98	0.00	12	1,122	
21	Age^2 + max fat^2 + lactating	40.22	0.00	11	1,150	
22	Age^2 + winter precip	79.68	0.00	9	1,193	
23	Age^2 + year	80.91	0.00	11	1,191	

[a] Indicates model ranks based on $\Delta QAIC_c$ scores when all models for (Φ, *p*, and ψ) are evaluated together.
[b] Difference between $QAIC_c$ value of current model and model with the lowest $QAIC_c$ value.
[c] $QAIC_c$ weight, which is defined as the relative likelihood of a model given the data and set of models.
[d] Number of parameters in the model.
[e] Deviance defined as the difference in –2log(likelihood) between the current model and the saturated model.

precipitation (Fig. 2A). The influence of summer precipitation was included in the suite of top models; however, the parameter estimates indicated a weak effect, with 95% *CI*s overlapping 0 (Table 3). A quadratic effect of age was present in all the top models, with the probability of becoming pregnant increasing until individuals reached prime age, then stabilizing or possibly decreasing above age 10 (Fig. 2B).

Body condition.—Female condition (e.g., body fat) had a strong influence on the probability of transitioning to pregnant, especially for low levels of max fat (Fig. 2C). Parameter estimates indicate a threshold level of max fat; thus once an individual acquired an intermediate level of max fat, probability of transitioning to pregnancy was high, >90%. Nonlactating individuals reached that threshold at lower levels of max fat than did lactating individuals. Once that threshold level was reached, there was little difference in transition probability between lactating and nonlactating individuals.

DISCUSSION

Energetic costs of gestation or lactation did not influence survival in this population of elk. Nonetheless, costs associated with lactation did result in a lower probability of reproducing the following year. This observed trade-off is consistent with life-history strategies of other long-lived species, which often maximize lifetime reproductive success through high, and less variable, adult survival, and more-variable reproductive output (Hamel et al. 2010). This life-history strategy resulted in a trade-off between current and future reproductive effort and no evidence of a trade-off between survival and reproduction. Indeed, survival has been reported to be the last vital rate of

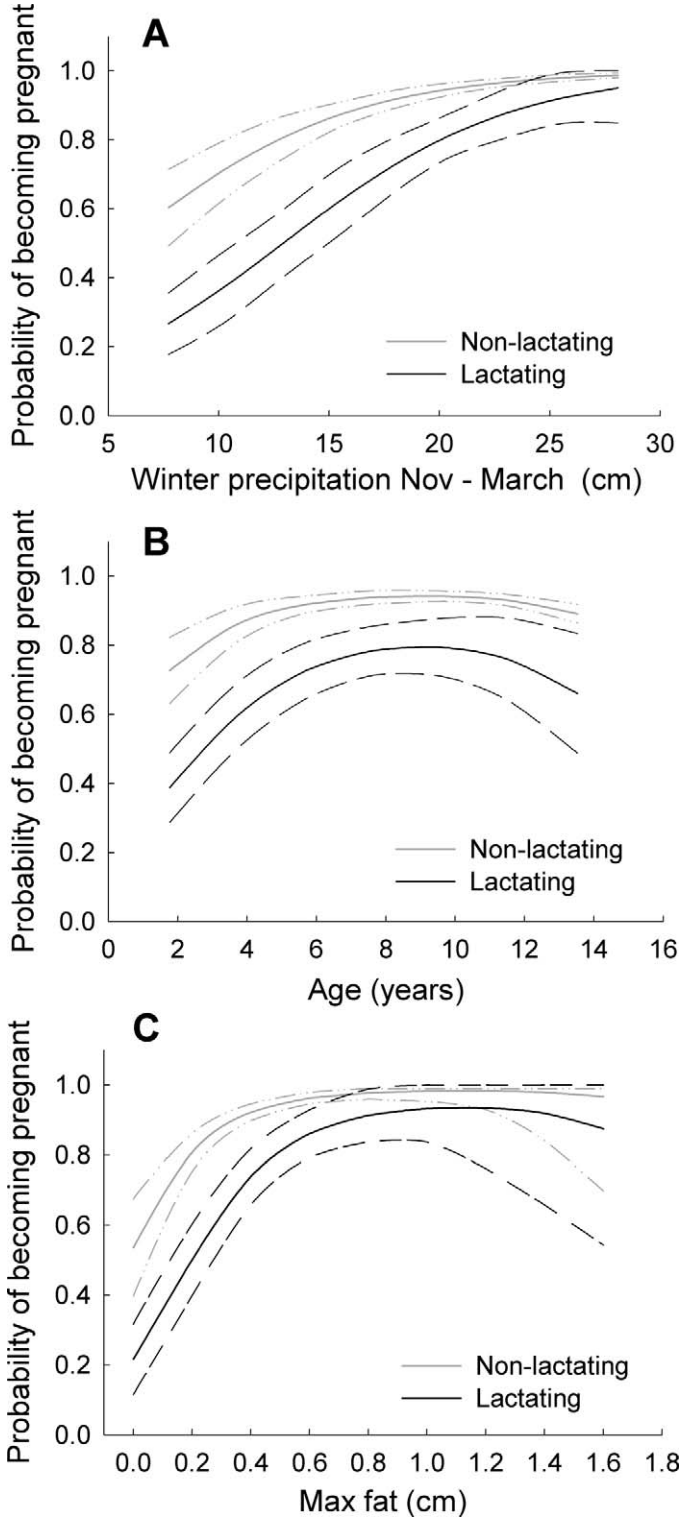

Fig. 2.—The influence of A) winter precipitation, B) age, and C) body condition (max fat) on the probability of transitioning to a pregnant state. This effect was modeled for individuals lactating or nonlactating at time of capture. Lactation at time of capture is used as an index of recruitment. Age is a continuous covariate, and max fat refers to the depth of subcutaneous rump fat, used as an index of body condition. Values were generated from model-averaged parameter estimates ± *SE* (Table 2) from adult female elk (*Cervus elaphus*) on the Starkey Experimental Forest and Range, La Grande, Oregon, 2001–2005. Covariate β was back-transformed using the logit-link function to generate effect plots.

populations to be affected by resource limitation (Eberhardt 1985).

A positive relationship between reproduction and survival, which was attributed to heterogeneity in individual quality, has been reported in other studies. Pregnant individuals had some social, physiological, or genetic advantage in resource acquisition or allocation; therefore they could consistently become pregnant (Cam et al. 2002; Hamel et al. 2009; Le Bohec et al. 2007). We did not detect a positive relationship between pregnancy and survival or between pregnancy and future reproduction. Nonetheless, we did find that the inclusion of individual variation (age, body condition, and recruitment) in models of transition probability greatly improved model performance over those containing only environmental variation (year or precipitation). Age and body condition are components of individual quality, which in turn affects breeding probability (Hamel et al. 2009; Moyes et al. 2009). Body condition, or max fat, was a strong predictor of whether an individual became pregnant; however, in our models max fat levels did not influence adult survival. This result indicates that suboptimal levels of max fat may translate to reduction in reproductive effort within a given year, but not necessarily a reduction in survival (Bardsen et al. 2010, 2011; Festa-Bianchet and Jorgenson 1998). Lactating individuals were less likely to become pregnant the following year than were nonlactating individuals. Nonetheless, once a threshold level of max fat was reached, probabilities became constant and there was no longer any observed cost associated with lactation. Individuals with low levels of max fat had much lower probabilities of becoming pregnant; this relationship was even more pronounced with the inclusion of lactation. Individuals that were in poor condition and had reared an offspring were less likely to become pregnant than those in even moderate condition. These results highlight the additive, negative effect that previous reproductive effort and low resource availability can have on future reproduction (Cook et al. 2004; Gerhart et al. 1997; Mautz 1978).

This population exhibited fluctuations in pregnancy rates in accordance with variation in winter precipitation the previous year. Precipitation during winter and early spring is tied to forage availability in the spring and summer (Derner et al. 2008), which influenced female condition and recruitment of offspring (Parker et al. 2009; Tollefson et al. 2010). In this ecosystem the majority of annual precipitation occurs as winter snow (Stewart et al. 2002); thus winter precipitation strongly reflects resource availability during spring and summer. The negative effect of lactation on pregnancy is evident during years with low levels of winter precipitation; however, at higher levels of winter precipitation the negative costs of lactation were eliminated, ostensibly because of effects on plant growth the following spring. These results also indicate that in years with increased resource availability individuals can overcome costs associated with lactation.

The overall probability of becoming pregnant within this population was strongly influenced by the amount of available resources an individual could acquire and store as fat. In years

Table 3.—Model-averaged parameter estimates (β) from top-ranked models (see Table 2) predicting survival and probability of transitioning to pregnant for North American elk (*Cervus elaphus*) on the Starkey Experimental Forest and Range, La Grande, Oregon, 2001–2005. Reproductive output was identified by whether an individual was pregnant or lactating in the current year. Lactation was used as an index of recruitment. Age is a continuous time-varying covariate. Winter precip refers to winter–spring precipitation (November–March), and summer precip to summer precipitation (July–September). Precipitation was included in the models as an index to summer resource availability. The influence of female condition was measured through depth of maximum rump fat (max fat).

				95% *CI*	
Model	Covariate	β	*SE*	Lower	Upper
Survival	Intercept	2.44	0.28	1.89	3.00
	Age	−0.47	0.15	−0.77	−0.17
	Age^2	−0.01	0.04	−0.09	0.07
	Winter precip	−0.20	0.31	−0.81	0.41
	Summer precip	0.08	0.20	−0.30	0.46
	Pregnant	−0.02	0.12	−0.24	0.21
	Lactating	0.01	0.06	−0.10	0.12
	Max fat	−0.001	0.04	−0.08	0.08
Transition	Intercept	1.73	0.24	1.25	2.21
	Age	0.90	0.23	0.45	1.35
	Age^2	−0.53	0.13	−0.78	−0.28
	Max fat	1.30	0.30	0.71	1.90
	Max fat^2	−0.25	0.15	−0.53	0.04
	Lactating	−0.72	0.20	−1.12	−0.32
	Winter precip	0.99	0.17	0.65	1.33
	Pregnant*lactating	0.01	0.10	−0.19	0.21
	Max fat*lactating	0.06	0.19	−0.30	0.42
	Summer precip	0.05	0.09	−0.13	0.24
	Pregnant	0.01	0.12	−0.22	0.25

when resources were limited, individuals likely would not gain adequate fat levels for both survival and reproduction; as a result limited fat stores might 1st be allocated to adult survival, over future reproduction, reducing the probability of becoming pregnant (Bardsen et al. 2010, 2011). Moreover, the additional energy expenditure required to recruit an offspring would result in further reduction in body condition (Clutton-Brock et al. 1983), strengthening the effect for females rearing offspring. In situations where populations experience some degree of resource limitation and fat gains are suboptimal, successful reproduction in consecutive years would be less likely (Clutton-Brock and Coulson 2002; Stewart et al. 2005; White et al. 1997), and costs associated with reproduction would be more pronounced (Clutton-Brock et al. 1987).

Elk on Starkey were fed a maintenance diet of alfalfa hay during winter; thus effects of resource acquisition on reproduction and survival are specific to spring, summer, and autumn (Stewart et al. 2005). Therefore, we have controlled for effects of winter with our experimental design (Stewart et al. 2005). Mautz (1978) indicated that winter forage reduces the rate and amount of body stores used by females during winter, rather than individuals acquiring body stores during that season. We documented substantial individual variation and annual variation in body condition resulting from resource acquisition during spring, summer, and autumn. In strongly seasonal environments large mammals, including elk (Hudson and Haigh 2002), reduce intake rates voluntarily during winter, even when provided ad libitum access to food (Parker et al. 2009). Therefore, elk experienced a cost of reproduction indicated by lower reproduction the following year. Those effects we documented from differences in acquisition of resources likely are conservative compared with free-ranging populations that experience greater nutritional restriction during winter. Recent research has documented the importance of summer nutrition on vital rates of populations (Bender et al. 2008; Stewart et al. 2005; Tollefson et al. 2010).

Age also influenced the probability of transitioning to pregnancy; younger individuals were less likely to become pregnant than prime-age individuals. This observation is consistent with those from other studies of ungulates (Côté and Festa-Bianchet 2001; Moyes et al. 2011; Stewart et al. 2005; Tavecchia et al. 2005). Younger individuals experienced a more-pronounced negative effect of lactation, which is more likely to result in a trade-off between current and future reproduction, skipping reproduction if they had successfully reproduced the previous year. That relationship became less pronounced as individuals aged. Nonetheless, there was evidence for a decline in pregnancy as individuals passed prime age, indicating the possibility of senescence in reproductive output with age.

The finding of a negative cost associated with lactation but not with gestation supports previous work that identified lactation as the more costly component of reproduction (Clutton-Brock et al. 1989; Parker et al. 2009). In general, energetic costs associated with gestation are not as great as those associated with lactation (Barboza et al. 2009; Parker et al. 2009). Individuals may consistently become pregnant if they were unsuccessful in rearing young. Thus, costs of reproduction might not become evident unless offspring survive and prolonged lactation occurs. This effect is an

important consideration when studying reproductive trade-offs and modeling populations dynamics of large mammals. If the measure of reproduction does not encompass the full cost to the individual, then it is possible to underestimate the effect.

Our findings suggest that in long-lived species, such as elk, costs associated with reproduction result in trade-offs between current and future reproduction with survival remaining relatively constant. Indeed this phenomenon also has been observed in Adélie penguins (*Pygoscelis adeliae*—Lescroel et al. 2009), red deer (*C. elaphus*—Moyes et al. 2011), reindeer (*Rangifer tarandus*—Bardsen et al. 2008), bighorn sheep (*Ovis canadensis*—Festa-Bianchet et al. 1998), and other large herbivores (see review in Gaillard et al. 2000). These results are consistent with risk-sensitive reproductive allocation (Bardsen et al. 2008, 2010) and support a life-history strategy that tends to maximize adult survival, resulting in greater variability in reproductive output. The potential for trade-offs between current and future reproduction is an important consideration when making predictions about population trajectories and determining how changes in resource availability influence population demographics. Understanding trade-offs (or lack thereof) associated with various life-history strategies, and the corresponding influence of individual and environmental variation, not only allows for the identification of potential fitness consequences of those trade-offs to the individual but also demographic consequences for the population.

Acknowledgments

We appreciate the assistance of Starkey Project personnel, especially those involved with collection of data and handling animals, particularly B. L. Dick and R. Kennedy. Also a special thanks to E. Blomberg for his assistance with data analysis and interpretation. R. T. Bowyer provided helpful comments on the manuscript. Funding for this project was provided by the Starkey Project, Pacific Northwest Field Station, United States Forest Service, the Rocky Mountain Elk Foundation, and the Rob and Bessie Welder Wildlife Foundation. Support for this project was provided by the Institute of Arctic Biology at the University of Alaska Fairbanks and the Department of Natural Resources and Environmental Science at the University of Nevada Reno.

Literature Cited

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's information criterion. Journal of Wildlife Management 74:1175–1178.

Barboza, P., K. Parker, and I. Hume. 2009. Integrative wildlife nutrition. Springer, Berlin, Germany.

Bardsen, B. J., P. Fauchald, T. Tveraa, K. Langeland, N. G. Yoccoz, and R. A. Ims. 2008. Experimental evidence of a risk-sensitive reproductive allocation in a long-lived mammal. Ecology 89:829–837.

Bardsen, B. J., J. A. Henden, P. Fauchald, T. Tveraa, and A. Stien. 2011. Plastic reproductive allocation as a buffer against environmental stochasticity—linking life history and population dynamics to climate. Oikos 120:245–257.

Bardsen, B. J., and T. Tveraa. 2012. Density-dependence vs. density-independence—linking reproductive allocation to population abundance and vegetation greenness. Journal of Animal Ecology 81:364–376.

Bardsen, B. J., T. Tveraa, P. Fauchald, and K. Langeland. 2010. Observational evidence of risk-sensitive reproductive allocation in a long-lived mammal. Oecologia 162:627–639.

Bender, L. C., J. G. Cook, R. C. Cook, and P. B. Hall. 2008. Relations between nutritional condition and survival of North American elk Cervus elaphus. Wildlife Biology 14:70–80.

Brownie, C., J. E. Hines, J. D. Nichols, K. H. Pollock, and J. B. Hestbeck. 1993. Capture–recapture studies for multiple strata including non-Markovian transitions. Biometrics 49:1173–1187.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer, New York.

Cam, E., J. E. Hines, J. Y. Monnat, J. D. Nichols, and E. Danchin. 1998. Are adult nonbreeders prudent parents? The Kittiwake model. Ecology 79:2917–2930.

Cam, E., W. A. Link, E. G. Cooch, J. Y. Monnat, and E. Danchin. 2002. Individual covariation in life-history traits: seeing the trees despite the forest. American Naturalist 159:96–105.

Choquet, R., J. D. Lebreton, O. Gimenez, A. M. Reboulet, and R. Pradel. 2009. U-CARE: utilities for performing goodness of fit tests and manipulating capture–recapture data. Ecography 32:1071–1074.

Clutton-Brock, T. H. 1982. The red deer of Rhum. Natural History 91:42–47.

Clutton-Brock, T. H., S. D. Albon, and F. E. Guinness. 1987. Interactions between population density and maternal characteristics affecting fecundity and juvenile survival in red deer. Journal of Animal Ecology 56:857–871.

Clutton-Brock, T. H., S. D. Albon, and F. E. Guinness. 1989. Fitness costs of gestation and lactation in wild mammals. Nature 337:260–262.

Clutton-Brock, T. H., and T. Coulson. 2002. Comparative ungulate dynamics: the devil is in the detail. Philosophical Transactions of the Royal Society of London, B. Biological Sciences 357:1285–1298.

Clutton-Brock, T. H., F. E. Guinness, and S. D. Albon. 1983. The cost of reproduction to red deer hinds. Journal of Animal Ecology 52:367–383.

Cook, J. G., et al. 2004. Effects of summer–autumn nutrition and parturition date on reproduction and survival of elk. Wildlife Monographs155:1–61.

Côté, S. D., and M. Festa-Bianchet. 2001. Reproductive success in female mountain goats: the influence of age and social rank. Animal Behaviour 62:173–181.

Coulson, T., et al. 2001. Age, sex, density, winter weather, and population crashes in Soay sheep. Science 292:1528–1531.

Davidson, G. A., B. K. Johnson, J. H. Noyes, B. L. Dick, and M. J. Wisdom. 2012. Effect of archer density on elk pregnancy rates and conception dates. Journal of Wildlife Management. http://onlinelibrary.wiley.com/doi/10.1002/jwmg.411/full

Derner, J. D., B. W. Hess, R. A. Olson, and G. E. Schuman. 2008. Functional group and species responses to precipitation in three semi-arid rangeland ecosystems. Arid Land Research and Management 22:81–92.

Doughty, P., and R. Shine. 1997. Detecting life history trade-offs: measuring energy stores in "capital" breeders reveals costs of reproduction. Oecologia 110:508–513.

Drent, R. H., and S. Daan. 1980. The prudent parent—energetic adjustments in avian breeding. Ardea 68:225–252.

EBERHARDT, L. L. 1985. Assessing the dynamics of wild populations. Journal of Wildlife Management 49:997–1012.

FESTA-BIANCHET, M., AND S. D. CÔTÉ. 2008. Mountain goats: ecology, behavior, and conservation of an alpine ungulate. Island Press, Washington, D.C.

FESTA-BIANCHET, M., J. M. GAILLARD, AND J. T. JORGENSON. 1998. Mass- and density-dependent reproductive success and reproductive costs in a capital breeder. American Naturalist 152:367–379.

FESTA-BIANCHET, M., AND J. T. JORGENSON. 1998. Selfish mothers: reproductive expenditure and resource availability in bighorn ewes. Behavioral Ecology 9:144–150.

GAILLARD, J. M., M. FESTA-BIANCHET, N. G. YOCCOZ, A. LOISON, AND C. TOIGO. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31:367–393.

GAILLARD, J. M., AND N. G. YOCCOZ. 2003. Temporal variation in survival of mammals: a case of environmental canalization? Ecology 84:3294–3306.

GERHART, K. L., D. E. RUSSELL, D. VAN DE WETERING, R. G. WHITE, AND R. D. CAMERON. 1997. Pregnancy of adult caribou (Rangifer tarandus): evidence for lactational infertility. Journal of Zoology (London) 242:17–30.

GLENN, E. M., R. G. ANTHONY, E. D. FORSMAN, AND G. S. OLSON. 2011. Local weather, regional climate, and annual survival of the northern spotted owl. Condor 113:159–176.

GREEN, W. C. H. 1990. Reproductive effort and associated costs in bison (*Bison bison*): do older mothers try harder? Behavioral Ecology 1:148–160.

HADLEY, G. L., J. J. ROTELLA, AND R. A. GARROTT. 2007. Evaluation of reproductive costs for Weddell seals in Erebus Bay, Antarctica. Journal of Animal Ecology 76:448–458.

HAMEL, S., S. D. CÔTÉ, J. M. GAILLARD, AND M. FESTA-BIANCHET. 2009. Individual variation in reproductive costs of reproduction: high-quality females always do better. Journal of Animal Ecology 78:143–151.

HAMEL, S., J. M. GAILLARD, N. G. YOCCOZ, A. LOISON, C. BONENFANT, AND S. DESCAMPS. 2010. Fitness costs of reproduction depend on life speed: empirical evidence from mammalian populations. Ecology Letters 13:915–935.

HUDSON, R. J., AND J. C. HAIGH. 2002. Physical and physiological adaptations. Pp. 199–257 in North American elk: ecology and management (D. E. Toweill and J. W. Thomas, eds.). Smithsonian Institution Press, Washington, D.C.

JOHNSON, J. B., AND K. S. OMLAND. 2004. Model selection in ecology and evolution. Trends in Ecology & Evolution 19:101–108.

KEECH, M. A., R. T. BOWYER, J. M. VER HOEF, R. D. BOERTJE, B. W. DALE, AND T. R. STEPHENSON. 2000. Life-history consequences of maternal condition in Alaskan moose. Journal of Wildlife Management 64:450–462.

KIE, J. G., T. R. BOWYER, AND K. M. STEWART. 2003. Ungulates in western coniferous forests: habitat relationships, population dynamics, and ecosystem processes. Pp. 296–340 in Mammal community dynamics: management and conservation in the coniferous forests of western North America (C. J. Zabel and R. G. Anthony, eds.). Cambridge University Press, Cambridge, United Kingdom.

LE BOHEC, C., ET AL. 2007. Population dynamics in a long-lived seabird: I. Impact of breeding activity on survival and breeding probability in unbanded king penguins. Journal of Animal Ecology 76:1149–1160.

LEBRETON, J.-D., K. P. BURNHAM, J. CLOBERT, AND D. R. ANDERSON. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62:67–118.

LESCROEL, A., K. M. DUGGER, G. BALLARD, AND D. G. AINLEY. 2009. Effects of individual quality, reproductive success and environmental variability on survival of a long-lived seabird. Journal of Animal Ecology 78:798–806.

LOMNICKI, A. 1978. Individual differences between animals and natural regulation of their numbers. Journal of Animal Ecology 47:461–475.

MAUTZ, W. W. 1978. Sledding on a bushy hillside: the fat cycle in deer. Wildlife Society Bulletin 6:88–90.

MCCULLOUGH, D. R. 1979. The George Reserve deer herd: population ecology of a K-selected species. University of Michigan Press, Ann Arbor.

MCCULLOUGH, D. R. 1999. Density dependence and life-history strategies of ungulates. Journal of Mammalogy 80:1130–1146.

MOYES, K., T. COULSON, B. J. T. MORGAN, A. DONALD, S. J. MORRIS, AND T. H. CLUTTON-BROCK. 2006. Cumulative reproduction and survival costs in female red deer. Oikos 115:241–252.

MOYES, K., B. J. T. MORGAN, A. MORRIS, S. J. MORRIS, T. H. CLUTTON-BROCK, AND T. COULSON. 2009. Exploring individual quality in a wild population of red deer. Journal of Animal Ecology 78:406–413.

MOYES, K., B. J. T. MORGAN, A. MORRIS, S. J. MORRIS, T. H. CLUTTON-BROCK, AND T. COULSON. 2011. Individual differences in reproductive costs examined using multi-state methods. Journal of Animal Ecology 80:456–465.

NICHOLS, J. D., J. E. HINES, K. H. POLLOCK, R. L. HINZ, AND W. A. LINK. 1994. Estimating breeding proportions and testing hypotheses about costs of reproduction with capture–recapture data. Ecology 75:2052–2065.

NICHOLS, J. D., AND W. L. KENDALL. 1995. The use of multi-state capture–recapture models to address questions in evolutionary ecology. Journal of Applied Statistics 22:835–846.

NOYES, J. H., R. G. SASSER, B. K. JOHNSON, L. D. BRYANT, AND B. ALEXANDER. 1997. Accuracy of pregnancy detection by serum protein (PSPB) in elk. Wildlife Society Bulletin 25:695–698.

NUSSEY, D. H., L. E. B. KRUUK, A. MORRIS, M. N. CLEMENTS, J. M. PEMBERTON, AND T. H. CLUTTON-BROCK. 2009. Inter- and intrasexual variation in aging patterns across reproductive traits in a wild red deer population. American Naturalist 174:342–357.

PARKER, K. L., P. S. BARBOZA, AND M. P. GILLINGHAM. 2009. Nutrition integrates environmental responses of ungulates. Functional Ecology 23:57–69.

ROWLAND, M. M., L. D. BRYANT, B. K. JOHNSON, J. H. NOYES, M. J. WISDOM, AND J. W. THOMAS. 1997. The Starkey project: history, facilities, and data collection methods for ungulate research. United States Department of Agriculture, Forest Service, Technical Report PNW-GTR 396:1–62.

SIKES, R. S., W. L. GANNON, AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 92:235–253.

STEARNS, S. C. 1992. The evolution of life histories. Oxford University Press, New York.

STEPHENSON, T. R., K. J. HUNDERTMARK, C. C. SCHWARTZ, AND V. VAN BALLENBERGHE. 1998. Predicting body fat and body mass in moose with ultrasonography. Canadian Journal of Zoology 76:717–722.

STEWART, K. M., R. T. BOWYER, B. L. DICK, B. K. JOHNSON, AND J. G. KIE. 2005. Density-dependent effects on physical condition and reproduction in North American elk: an experimental test. Oecologia 143:85–93.

STEWART, K. M., R. T. BOWYER, J. G. KIE, N. J. CIMON, AND B. K. JOHNSON. 2002. Temporospatial distributions of elk, mule deer, and cattle: resource partitioning and competitive displacement. Journal of Mammalogy 83:229–244.

STEWART, K. M., R. T. BOWYER, R. W. RUESS, B. L. DICK, AND J. G. KIE. 2006. Herbivore optimization by North American elk: consequences for theory and management. Wildlife Monographs 167:1–24.

TAVECCHIA, G., ET AL. 2005. Predictors of reproductive cost in female Soay sheep. Journal of Animal Ecology 74:201–213.

TOIGO, C., J. M. GAILLARD, D. GAUTHIER, I. GIRARD, J. P. MARTINOT, AND J. MICHALLET. 2002. Female reproductive success and costs in an alpine capital breeder under contrasting environments. Ecoscience 9:427–433.

TOLLEFSON, T. N., L. A. SHIPLEY, W. L. MYERS, D. H. KEISLER, AND N. DASGUPTA. 2010. Influence of summer and autumn nutrition on body condition and reproduction in lactating mule deer. Journal of Wildlife Management 74:974–986.

VAN NOORDWIJK, A. J., AND G. DE JONG. 1986. Acquisition and allocation of resources: their influence on variation in life history tactics. American Naturalist 128:137–142.

WELADJI, R. B., ET AL. 2008. Heterogeneity in individual quality overrides costs of reproduction in female reindeer. Oecologia 156:237–247.

WHITE, G. C., AND K. P. BURNHAM. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:120–139.

WHITE, R. G., J. E. ROWELL, AND W. E. HAUER. 1997. The role of nutrition, body condition and lactation on calving success in muskoxen. Journal of Zoology (London) 243:13–20.

WILLIAMS, G. C. 1966. Adaptation and natural selection. Princeton University Press, Princeton, New Jersey.

ZAR, J. H. 2010. Biostatistical analysis. 5th ed. Prentice-Hall, New Jersey.

Submitted 21 March 2012. Accepted 13 July 2012.

Associate Editor was Christine R. Maher.