



Research Article

Cumulative costs of reproduction in a long-lived ungulate

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Associate Editor was Burton Lim

Abstract

Cumulative costs of reproduction are predicted by life-history theories of aging, but empirical support for cumulative costs of reproduction in ungulates is limited. Examinations of the relationship between previous reproductive effort and future reproductive output are often limited to successive years. We analyzed pregnancy status, lactation duration, and age class of Elk (*Cervus canadensis*) in Utah, United States, from 2019 to 2022 to better understand the relationship between previous reproductive effort and future reproductive output, particularly in nonsuccessive years. Pregnancy status 1 year prior, pregnancy status 2 years prior, and age had no effect on the likelihood of pregnancy in Elk. However, lactation duration 1 year prior and lactation duration 2 years prior had a negative effect on the likelihood of pregnancy. The best-fitting model to explain the relationship between pregnancy status and previous lactation was the positive interaction between lactation duration 1 year prior and lactation duration 2 years prior. The results of our study suggest long-lasting (i.e., multiple-year), cumulative costs of reproduction can influence reproductive output in female Elk, but differences in individual quality may have an even greater influence. High-quality individuals may be able to override the costs of reproduction and minimize reproductive trade-offs.

Key words: age, *Cervus canadensis*, Elk, gestation, individual quality, lactation, reproductive costs, ungulates, Utah.

Reproduction is an energetically expensive activity for female ungulates and has consequences relative to individual fitness (Clutton-Brock et al. 1989; Pekins et al. 1998; Hamel and Côté 2008). For example, energy costs are greater in pregnant individuals than in nonpregnant individuals (Mauget et al. 1997; Pekins et al. 1998). Following parturition, energy costs are further increased during lactation (Gittleman and Thompson 1988). Lactating ungulates spend more time foraging than their nonlactating counterparts and have lower body condition after the weaning period (Ruckstuhl and Festa-Bianchet 1998; Ruckstuhl and Neuhaus 2002; Hamel and Côté 2008; Cook et al. 2013; Simard et al. 2014). Reductions in body condition can result in additional fitness costs including reduced survival, reduced likelihood of pregnancy, delayed parturition, and reduced mass of offspring (Birgersson and Ekvall 1997; Mduma et al. 1999; Cook et al. 2004a; Tollefson et al. 2010).

To maximize fitness while experiencing the trade-offs of reproduction, long-lived ungulates often exhibit a life-history strategy of consistently high adult survival paired with variable reproductive output (Gaillard and Yoccoz 2003; Hamel et al. 2010). Adjusting the number of offspring produced in a given litter likely allows females to maintain energy reserves (Gaillard et al. 2000; Hamel et al. 2010; Boertje et al. 2019). Female ungulates in poor condition tend to produce reduced numbers of offspring or fail to produce offspring at all (Keech et al. 2000; Cook et al. 2004b; Tollefson et al. 2010). Correlates of body condition such as age, precipitation, and population density

can also influence the quantity of offspring produced (Coulson et al. 2000; Cook et al. 2013; Boertje et al. 2019). An additional factor that can influence reproductive output is reproductive effort in the previous year (for species that reproduce once a year). Typically, a negative relationship exists between reproductive effort in the previous year and the number of offspring produced by female ungulates in the subsequent year (Clutton-Brock et al. 1983; Gerhart et al. 1997; Stewart et al. 2005; Morano et al. 2013; Boertje et al. 2019). However, reproductive effort in the previous year does not always impact subsequent reproduction, or may only have an impact on individuals in poor condition (Albon et al. 1986; Festa-Bianchet and Côté 2008; Hamel et al. 2009; Markussen et al. 2018). Less is known about the relationship between prior reproductive effort and future reproductive output in nonsuccessive years—potential cumulative costs.

It seems plausible that long-lasting, cumulative costs of reproduction could influence reproductive output over multiple years, especially in marginal environments where nutrition is limited. Costs of reproduction can be mitigated when individuals are in good condition, potentially indicating that costs can be magnified when individuals are in poor condition (Hamel et al. 2009). Cumulative costs of reproduction are also predicted by various life-history theories related to aging (Lemaître et al. 2015). For example, disposable soma theory posits that when resources are allocated toward reproduction in lieu of maintenance, accumulated errors in somatic cells may reduce future reproductive output (Kirkwood 1977;

Received: January 26, 2023; Editorial Decision: June 12, 2024; Accepted: July 1, 2024

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Kirkwood and Rose 1991; Kirkwood and Austad 2000). Moreover, antagonistic pleiotropy theory suggests that alleles benefiting reproduction early in life may have a negative effect on reproduction later in life (Williams 1957). Despite the potential for cumulative costs of reproduction, our understanding of the relationship between previous reproductive effort and future reproductive output in ungulates is often limited to successive years (Festa-Bianchet and Côté 2008; Hamel et al. 2009; Morano et al. 2013; Markussen et al. 2018; Boertje et al. 2019).

Our objective was to better understand the relationship between previous reproductive effort, future reproductive output, and age in long-lived ungulates. We used free-ranging, female Elk (*Cervus canadensis*) as an initial model. The relationship between previous reproductive effort and future reproductive output has previously been examined in Elk, but only for successive years and only in a captive population with access to supplemental nutrition (Stewart et al. 2005; Morano et al. 2013). Physical and behavioral differences between captive and free-ranging animals (including differences in reproductive behavior) have been reported across various taxa, exemplifying the need for studies in both systems (Lambrechts et al. 1999; Hosey 2005; Mathews et al. 2005; Burns et al. 2009; Clubb et al. 2009). Reproductive tactics may also be more pronounced in animals without access to supplemental nutrition, particularly in marginal environments where nutrition is limited. We hypothesized that cumulative costs of reproduction would be apparent in female Elk, as predicted by life-history theories of aging (Williams 1957; Kirkwood 1977; Kirkwood and Rose 1991; Kirkwood and Austad 2000). Nevertheless, we hypothesized that cumulative costs of reproduction would only be apparent when examining the costs of lactation—not gestation. Previous gestation effort did not influence the likelihood of pregnancy for captive Elk when monitored over successive years (Morano et al. 2013). Previous lactation effort, however, did influence the likelihood of pregnancy (Stewart et al. 2005; Morano et al. 2013). Consequently, we predicted that pregnancy status 1 year prior and 2 years prior would have no influence on the likelihood of pregnancy, but lactation duration 1 year prior and 2 years prior would have a negative influence on the likelihood of pregnancy. We also predicted that age would have a negative influence on the likelihood of pregnancy (Cook et al. 2013). Regardless of the observed relationship, examining cumulative costs of reproduction will increase our understanding of population dynamics, reproductive trade-offs, and ungulate ecology.

Materials and methods.

Study area.

We completed this study in the Book Cliffs management unit (39.5°, -109.3°) of east-central Utah, United States. Located in the Colorado Plateau physiographic region, geographic features included cliff faces, ridges, valleys, and flatlands. Elevations in the study area ranged from approximately 1,675 to 2,590 m. Average annual precipitation was 21.8 cm and average annual temperature was 8.4 °C (PRISM Climate Group 2022). Habitat for Elk in the study area was considered marginal and included limited forage production on summer range (Utah Division of Wildlife Resources 2016). Precipitation has been identified as the limiting factor for the expansion of Quaking Aspen (*Populus tremuloides*) in the Book Cliffs and likely limited other vegetation as well (Sexton et al. 2006). Additional vegetation communities included sagebrush steppes (*Artemisia* spp.) and pine-juniper woodlands (*Pinus monophylla*-*Juniperus oteosperma*). Native and non-native ungulates were present in potential Elk habitat, including Bighorn Sheep (*Ovis canadensis*), Bison (*Bison bison*), Domestic Cattle (*Bos taurus*),

feral Domestic Horse (*Equus caballus*), Mule Deer (*Odocoileus hemionus*), and American Pronghorn (*Antilocapra americana*). Potential predators of Elk included Black Bear (*Ursus americanus*), Bobcat (*Lynx rufus*), Coyote (*Canis latrans*), and Mountain Lion (*Puma concolor*).

Determination of pregnancy status, lactation duration, and age.

We captured adult female Elk with the aid of an independent capture company (Helicopter Wildlife Services, Austin, Texas, or Quicksilver Air Inc., Peyton, Colorado) and the Utah Division of Wildlife Resources (Salt Lake City, Utah) during February of 2019 to 2022. Capture personnel performed all captures on public land using helicopter net-gunning or darting (Barrett et al. 1982; Krausman et al. 1985; McCorquodale et al. 1988). For dart captures, capture personnel induced immobilization using thiafentanil (10 mg/mL, Wildlife Pharmaceuticals, Laramie, Wyoming) and xylazine (300 mg/mL, Wildlife Pharmaceuticals) delivered in a barbed dart (type U, 1.5 mL, Pseudart, Williamsport, Pennsylvania). To reverse immobilization, capture personnel administered naltrexone (50 mg/mL, Wildlife Pharmaceuticals) and atipamezole (25 mg/mL, Wildlife Pharmaceuticals) intramuscularly.

Following capture, we fitted each animal with a tracking collar and determined its pregnancy status, lactation score, and age. Collars (G5-2DH, 657 g, Advanced Telemetry Systems, Isanti, Minnesota) used global positioning system (GPS) technology, recorded coordinates every 2 h, and produced very high frequency transmissions to allow for future monitoring. We determined pregnancy status using transabdominal ultrasonography (IBEX PRO, E.I. Medical Imaging, Loveland, Colorado) or radioimmunoassay of blood samples for pregnancy-specific protein B (PSPB; Utah Veterinary Diagnostics Lab, Logan, Utah; Stephenson et al. 1995; Bishop et al. 2007). Ultrasonography and PSPB results rarely differ when determining pregnancy status (Noyes et al. 1997; Duquette et al. 2012). Following a visual inspection of the udders, we assigned each animal a lactation score (0, 0.25, 0.5, 0.75, or 1) which estimated when lactation last occurred (Table 1). Physical characteristics of udders (e.g., swelling) have been used to determine if Elk lactated in the previous year and can aid investigations of reproductive effort (Cook et al. 2004b). We also estimated the age of each animal based on patterns of tooth eruption and wear (Quimby and Gaab 1957). To ensure relative accuracy of age estimates, we utilized experienced agers that previously estimated ages of Elk within 2 years of the true age nearly 80% of the time (Sergeyev et al. 2021). Notably, age-related impacts on mammalian reproduction tend to be best explained using age classes derived from reproductive thresholds

Table 1. Physical characteristics that corresponded with lactation scores assigned to female Elk during a visual inspection of the udders. Hair loss, lack of wax plugs (which typically seal the teat canal), and swelling were indicators of recent lactation. Lactation scores (0, 0.25, 0.5, 0.75, or 1) were an estimate of when lactation last occurred. All lactation scores were assigned during February of 2019 to 2022 in east-central Utah.

Lactation score	Physical characteristics
0	No evidence of recent lactation
0.25	Hair loss around teats, no wax plugs
0.5	Hair loss around teats, no wax plugs, swollen teats
0.75	Hair loss around teats, no wax plugs, swollen teats and mammary glands
1	Currently lactating

(Lemaître et al. 2020). Thus, we used age estimates to classify Elk as prime-age (2.5 to 14.5 years) or old-age (≥ 15.5 years) based on reproductive patterns displayed by Elk in the Rocky Mountains (Cook et al. 2013).

Supplemental determination of pregnancy status.

We attempted to recapture Elk in successive years, but recaptures failed to occur when animals dispersed to inaccessible areas or otherwise could not be located. In order to increase our sample size of individuals with a known pregnancy status over multiple years, we used GPS data to determine the pregnancy status of collared individuals that were not recaptured. Female ungulates reduce and localize movements following parturition, which allows for parturition events to be identified using movement-related metrics (DeMars et al. 2013; Peterson et al. 2018; Mohr et al. 2022; Hughes et al. 2024). We created a model that incorporated turning angle and home range size (minimum convex polygon) over the potential parturition period (1 May to 31 July) to predict the pregnancy status of collared Elk in our study area. To train and validate the model, we utilized GPS data from every Elk with a known pregnancy status in the study area during 2019 to 2022 ($n = 105$ individuals, 146 potential parturition periods). The best-performing iteration of the model used a mean turning angle threshold of 1.6 radians and a mean home range threshold of 0.35 km² over 2-day rolling intervals to correctly identify pregnancy status 90.4% of the time. Following validation, we used the best-performing iteration of the model to determine pregnancy status of an individual when ultrasonography or PSPB results were not available. All procedures were in compliance with the Institutional Animal Care and Use Committee at Brigham Young University (protocol 19-0202) and guidelines from the American Society of Mammalogists (Sikes et al. 2016).

Data analysis.

Because the efficacy of using lactation scores to estimate when lactation last occurred has not yet been reported, we validated the technique using juvenile survival data (Supplementary Data SD1) associated with a related project in our study area (with many of the same animals included in both studies). An in-depth description of juvenile capture methods and subsequent monitoring of juvenile survival can be found elsewhere (Turnley et al. 2022). We determined the relationship between the number of days offspring of a female survived in the previous year (modeled as 0 days survived if an individual was not pregnant) and her lactation score using a cumulative link mixed model. We included female age class as a fixed effect to account for age-related influences on offspring survival. In addition, we included individual and year as random effects to account for nonindependence of repeated individuals and temporal differences, respectively.

To determine the link between previous reproductive effort, future reproductive output, and age, we analyzed pregnancy status and lactation scores (Supplementary Data SD2 and SD3) using mixed-effects logistic regression models. We used 11 a priori models to examine the relationship between pregnancy status (coded as not pregnant = 0, pregnant = 1) and predictor variables related to previous pregnancies—pregnancy status 1 year prior, pregnancy status 2 years prior, and age class. Similarly, we used 11 a priori models to examine the relationship between pregnancy status and predictor variables related to previous lactation effort—lactation score 1 year prior, lactation score 2 years prior, and age class. We used separate analyses to examine pregnancy and lactation-related variables because not all predictor variables were known for every individual. In addition, we included individual and year as random effects in all logistic regression models. To determine the best-fitting model,

we used Akaike's Information Criterion adjusted for small sample sizes (AICc; Burnham and Anderson 2002). We considered all models with a $\Delta\text{AICc} < 2.0$ and a lack of uninformative parameters (i.e., parameters that did not improve model fit) to be competitive, using 85% confidence intervals (CIs) in all interpretations (Arnold 2010; Leroux 2019). In all analyses, we confirmed that relevant model assumptions were met (Stoltzfus 2011; Bürkner and Vuorre 2019). We analyzed all data using R version 4.3.1 (lme4, lmerTest, and ordinal packages; Bates et al. 2015; Kuznetsova et al. 2017; Christensen 2023; R Core Team 2023).

Results

We analyzed data from 128 determinations of pregnancy status, 66 lactation examinations, and 39 observations of offspring survival associated with 46 female Elk over 4 years. We determined 42 (32.8%) pregnancy statuses using ultrasonography, 36 (28.1%) using PSPB results, and 50 (39.1%) using movement metrics. Reproductive pauses were relatively common over the duration of the study. Of the 128 pregnancy statuses, 39 (30.5%) were associated with an individual that was not pregnant. Of the 13 Elk with a known pregnancy status for all 4 years of the study, only 2 (15.4%) individuals were pregnant all 4 years. Of the 66 lactation examinations, 6 (9.1%) resulted in a lactation score of 0, 39 (59.1%) in a lactation score of 0.25, 18 (27.3%) in a lactation score of 0.5, 3 (4.5%) in a lactation score of 0.75, and 0 in a lactation score of 1. There was a positive relationship between the number of days offspring of a female survived in the previous year and her lactation score ($\beta = 0.01$, $\text{SE} = 0.003$, $z_{37} = 3.23$, $P \leq 0.001$; Fig. 1). For every day the offspring of a female survived, there was a 1% increase in the odds that her lactation score would increase by 0.25 (proportional odds ratio = 1.01). Age estimates in our examination of the relationship between pregnancy status and previous pregnancies included 28 (59.6%) estimates associated with a prime-aged female and 19 (40.4%) estimates associated with an old-age female. Age estimates in our examination of the relationship between pregnancy status and previous lactation durations included 14 (35.9%) estimates associated with a prime-aged female and 25 (64.1%) estimates associated with an old-age female.

The best-fitting model to explain the relationship between pregnancy status and previous pregnancies was the null model (Table 2). The only other model with a $\Delta\text{AICc} < 2.0$ included age class as its only parameter, but age class was uninformative (85% CI = -1.58 to 0.61). Thus, the null model was the only competitive model. There was a negative relationship between the number of parameters in a model and its relative ranking. The lack of support for models with predictor variables indicated that pregnancy status 1 year prior, pregnancy status 2 years prior, and age class all had no impact on the likelihood of pregnancy.

The best-fitting model to explain the relationship between pregnancy status and previous lactation included the interaction between lactation score 1 year prior and lactation score 2 years prior (Table 3). CIs for the top model indicated that lactation score 1 year prior and lactation score 2 years prior both had negative influences on the likelihood of pregnancy, but the interaction between lactation score 1 year prior and lactation score 2 years prior was positive overall (Table 4). The only negative interaction between lactation score 1 year prior and lactation score 2 years prior was for individuals with no evidence of lactation 1 year prior (Fig. 2). Although the interaction was the only competitive model, the second and third highest ranking models included lactation score 1 year prior and lactation score 2 years prior as additive parameters. When lactation scores from both years were not included in the

same model, all models that contained lactation score 1 year prior were ranked higher than models that contained lactation score 2 years prior. Inclusion of age class as a parameter did not improve the ranking of any model, and the model with age class as its only parameter was the second lowest ranking model.

Discussion

Our results indicated that cumulative costs of reproduction were apparent in female Elk, but only when examining lactation costs. Previous pregnancy status had no impact on the likelihood of pregnancy. This result is consistent with prior work suggesting the costs of gestation for female Elk have no impact on future reproductive output (Morano et al. 2013). Lactation scores, which were indicative of how long offspring of a female survived in the previous year, allowed us to determine the influence of lactation duration. In addition, lactation scores were negatively related to pregnancy status,

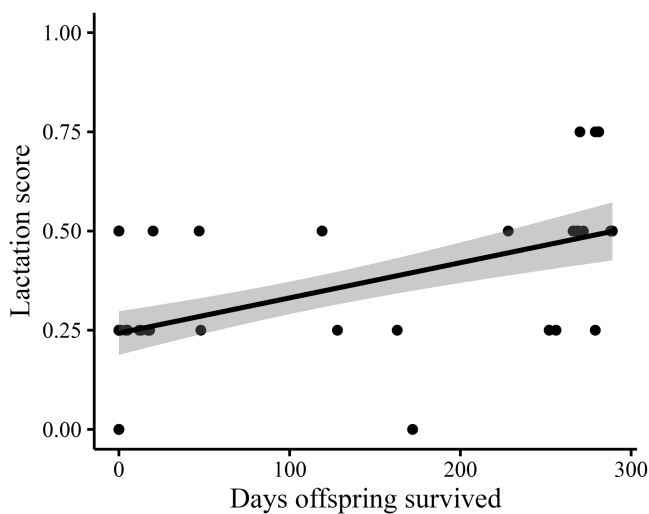


Fig. 1. Lactation score of female Elk in relation to the number of days a female's offspring survived in the previous year. Lactation scores, estimates of when lactation last occurred, were determined in February following a visual inspection of the udders. Shaded area represents an 85% CI. All lactation scores and survival monitoring took place during 2019 to 2022 in east-central Utah.

suggesting increased swelling and hair loss were not physiological preparations for future lactation (further validating the use of lactation scores). The negative relationship we observed between lactation duration 1 year prior and the likelihood of pregnancy was the same relationship displayed by captive Elk (Stewart et al. 2005; Morano et al. 2013). There was also a negative relationship between lactation duration 2 years prior and the likelihood of pregnancy. Although lactation duration 1 year prior was a better predictor of pregnancy status than lactation duration 2 years prior, our results suggest that the costs of lactation can restrict reproductive output for multiple years. Lactation is the most expensive period in a female ungulate reproductive cycle and evidence of cumulative costs of lactation further supports this principle (Clutton-Brock et al. 1989; Parker et al. 2009).

Although cumulative costs of lactation were apparent, individual quality likely had an even greater influence on the likelihood of pregnancy in Elk. The most supported model for pregnancy status included the interaction between lactation duration 1 year prior and lactation duration 2 years prior. Interestingly, the interaction was positive despite lactation-related parameters having negative effects when examined separately. A relatively long lactation duration (i.e., longer-lived offspring) in both of the previous 2 years increased the likelihood of pregnancy, whereas a relatively long lactation duration in just one of the previous 2 years decreased the likelihood of pregnancy. In other words, highly productive females tended to stay highly productive (as measured by pregnancy status and offspring survival) and relatively unproductive females tended to stay unproductive. Variation in individual quality has resulted in differential reproduction in other ungulates as well, with high-quality individuals consistently having greater reproductive success than lower-quality individuals (Festa-Bianchet et al. 1998; Weladji et al. 2008; Hamel et al. 2009). High-quality individuals may be able to "override" the costs of reproduction, minimizing the expected trade-offs associated with energetically expensive activities (Weladji et al. 2008). This theory has also been utilized to explain the positive relationship between reproductive effort and female survival displayed in certain ungulates (Moyes et al. 2006).

Various life-history theories related to aging postulate cumulative costs of reproduction, including disposable soma theory and antagonistic pleiotropy theory (Williams 1957; Kirkwood 1977; Kirkwood and Rose 1991; Kirkwood and Austad 2000). However, age was not an accurate predictor of pregnancy status in our study. This result

Table 2. Ranking of models utilized to examine pregnancy status of a female Elk as a function of pregnancy status 1 year prior ($Pregnancy_{(t-1)}$), pregnancy status 2 years prior ($Pregnancy_{(t-2)}$), and age class (age). Age classes include prime-age (2.5 to 14.5 years) and old-age (≥ 15.5 years). Ranking order based on Akaike's Information Criterion adjusted for small sample sizes (AICc). Statistics include the number of estimated parameters (K), log likelihood (LogL), change in AICc from the top model (ΔAIC_c), and model weight (w_i). All determinations of pregnancy status and age took place during February of 2019 to 2022 in east-central Utah.

Model	K	LogL	ΔAIC_c	w_i
Null	3	-24.83	0.00	0.39
Age	4	-24.63	1.99	0.14
$Pregnancy_{(t-2)}$	4	-24.68	2.10	0.14
$Pregnancy_{(t-1)}$	4	-24.69	2.12	0.14
$Pregnancy_{(t-1)} + Age$	5	-24.47	4.19	0.05
$Pregnancy_{(t-2)} + Age$	5	-24.54	4.34	0.05
$Pregnancy_{(t-1)} + Pregnancy_{(t-2)}$	5	-24.58	4.41	0.04
$Pregnancy_{(t-2)} \times Age + Pregnancy_{(t-2)} + Age$	6	-24.32	6.52	0.02
$Pregnancy_{(t-1)} \times Pregnancy_{(t-2)} + Pregnancy_{(t-1)} + Pregnancy_{(t-2)}$	6	-24.32	6.52	0.02
$Pregnancy_{(t-1)} \times Age + Pregnancy_{(t-1)} + Age$	6	-24.36	6.61	0.01
$Pregnancy_{(t-1)} + Pregnancy_{(t-2)} + Age$	6	-24.41	6.71	0.01

Table 3. Ranking of models utilized to examine pregnancy status of a female Elk as a function of lactation score 1 year prior ($Lactation_{(t-1)}$), lactation score 2 years prior ($Lactation_{(t-2)}$), and age class (age). Age classes include prime-age (2.5 to 14.5 years) and old-age (≥ 15.5 years). Ranking order based on Akaike's Information Criterion adjusted for small sample sizes (AICc). Statistics include the number of estimated parameters (K), log likelihood (LogL), change in AICc from the top model (ΔAIC_c), and model weight (w_i). All determinations of pregnancy status, lactation score, and age took place during February of 2019 to 2022 in east-central Utah.

Model	K	LogL	ΔAIC_c	w_i
$Lactation_{(t-1)} \times Lactation_{(t-2)} + Lactation_{(t-1)} + Lactation_{(t-2)}$	6	-16.11	0.00	0.68
$Lactation_{(t-1)} + Lactation_{(t-2)}$	5	-19.28	3.54	0.12
$Lactation_{(t-1)} + Lactation_{(t-2)} + Age$	6	-18.30	4.39	0.08
$Lactation_{(t-1)}$	4	-21.31	4.95	0.06
$Lactation_{(t-1)} + Age$	5	-20.74	6.45	0.03
$Lactation_{(t-1)} \times Age + Lactation_{(t-1)} + Age$	6	-19.48	6.74	0.02
$Lactation_{(t-2)}$	4	-23.26	8.85	0.01
Null	3	-24.79	9.42	0.01
$Lactation_{(t-2)} + Age$	5	-22.85	10.67	0.00
Age	4	-24.57	11.48	0.00
$Lactation_{(t-2)} \times Age + Lactation_{(t-2)} + Age$	6	-22.23	12.24	0.00

Table 4. Beta estimates (β), standard error (SE), and 85% confidence intervals (85% CIs) for each parameter in our best-fitting model examining pregnancy status of a female Elk as a function of lactation score 1 year prior, lactation score 2 years prior, and age class. All determinations of pregnancy status, lactation score, and age took place during February of 2019 to 2022 in east-central Utah.

Parameter	β	SE	85% CI
$Lactation_{(t-1)}$	-26.89	10.37	-41.81, -11.96
$Lactation_{(t-2)}$	-13.90	8.33	-25.90, -1.90
$Lactation_{(t-1)} \times Lactation_{(t-2)}$	62.12	27.07	23.15, 101.10

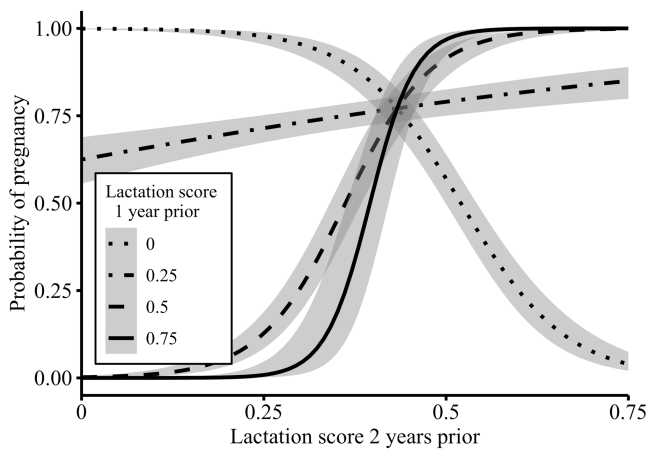


Fig. 2. Probability of pregnancy for female Elk in relation to the interaction between lactation score 1 year prior and lactation score 2 years prior. Lactation scores, estimates of when lactation last occurred, were determined in February following a visual inspection of the udders. Line type indicates lactation score 1 year prior and shaded areas represent 85% CIs. All lactation scores and pregnancy determinations took place during 2019 to 2022 in east-central Utah.

was surprising considering the age-related declines in pregnancy recorded elsewhere (Stewart et al. 2005; Cook et al. 2013; Bender and Piasecke 2019). We offer 3 potential explanations for the lack of age-specific impacts, but more work should be done to determine their validity. First, single-year reproductive pauses may generally

be sufficient to restore energy reserves of female ungulates regardless of age, essentially “resetting” the relationship between previous reproductive effort and future reproductive output. Reproductive pauses that lasted for more than a year occurred in only 4.9% of successive pregnancy examinations in our study. Similarly, reproductive pauses in Caribou (*Rangifer tarandus*) lasted for more than a year in only 5.0% of successive pregnancy examinations (Cameron 1994). Second, age-specific impacts may have been masked by nutritional constraints. Forage quality and quantity tend to be the predominant bottom-up regulators of reproductive output in ungulates (Parker et al. 1999, 2009). Considering that the Book Cliffs has minimal summer forage for Elk, the (presumably poor) condition of animals may have had a masking effect when attempting to elucidate the impacts of age (Utah Division of Wildlife Resources 2016). And third, the lack of age-specific impacts may have been due to limitations associated with our study. Although we utilized experienced agers and broad age classes, exact estimates of age can be difficult to determine from patterns of tooth eruption and wear (Hamlin et al. 2000). Repeated captures of individual Elk revealed that age estimates did not always reflect the true passage of time (Supplementary Data SD1–SD3). Moreover, age-related declines in pregnancy may not have aligned with the age classes used in our study. We used age classes based on reproductive patterns of Elk in neighboring states, but the onset of reproductive senescence in Elk can vary (Cook et al. 2013; Bender and Piasecke 2019). In addition, our analyses were reliant on a relatively small sample of individuals ($n = 46$). A larger sample size (i.e., greater statistical power) may have revealed age-specific impacts more consistent with the patterns of reproductive senescence typically displayed by Elk (Cook et al. 2013; Bender and Piasecke 2019).

Female ungulates utilize a variety of tactics to mitigate the costs of previous reproductive effort. As discussed, adjusting the number of offspring produced allows females to restore energy reserves and may limit the impact of cumulative costs of reproduction (Gaillard et al. 2000; Hamel et al. 2010; Boertje et al. 2019). Costs can even be transferred to offspring via a reduction in maternal allocation (Martin and Festa-Bianchet 2010). We provide evidence that the costs of reproduction can still impact reproductive output over multiple years despite cost mitigation efforts. However, we support the notion that individual quality may have an even greater influence on reproductive output than the costs of previous reproduction (Weladji et al. 2008; Hamel et al. 2009). While more work is required,

we offer a rare examination of reproductive costs in nonsuccessive years, providing insight into the reproductive tactics of long-lived ungulates.

Supplementary data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Raw data used to validate the efficacy of using lactation scores to estimate when lactation last occurred.

Supplementary Data SD2.—Pregnancy-related variables and corresponding raw data used to examine the costs of previous gestation effort.

Supplementary Data SD3.—Lactation-related variables and corresponding raw data used to examine the costs of previous lactation effort.

Acknowledgments

We thank Kaylee Draughon, Morgan Hinton, Daniel Sallee, Clint Sampson, and Levi Watkins for their assistance with data collection. Anna Moeller assisted with analytical interpretations.

Author contributions

MTT—investigation, formal analysis, writing (original draft, review, and editing); TAH—investigation, formal analysis, writing (review and editing); RTL—conceptualization, funding acquisition, investigation, writing (review and editing); KRH—funding acquisition, investigation, writing (review and editing); BRM—conceptualization, funding acquisition, investigation, writing (review and editing).

Funding

This study was financially supported by the American Society of Mammalogists, Brigham Young University, the Mule Deer Foundation, the Rocky Mountain Elk Foundation, Safari Club International, Sportsmen for Fish and Wildlife, and the Utah Division of Wildlife Resources.

Conflict of interest

None declared.

Data availability

All data required to replicate the results of this study are available as supplementary data.

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