Received: 15 March 2024 | Revised: 12 September 2024 | Accepted: 3 October 2024

DOI: 10.1002/jwmg.22690

THE JOURNAL OF WILDLIFE MANAGEMENT | THE WILDLIFE SOCIETY

RESEARCH ARTICLE

Variability and correlations among vital rates and their influence on population growth in mule and black-tailed deer

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Abstract

To reverse range-wide population declines, managers of black-tailed and mule deer (*Odocoileus hemionus*) require information on the vital rates and life stages most influential to population growth to target effective management actions. We extracted black-tailed and mule deer vital rates from a range-wide literature review and used hierarchical models to summarize vital rates, their variability, and how they correlate with one another. We then used matrix models and life-stage simulation analysis to determine the individual vital rates that contributed most to annual population growth rate (i.e., lambda). Annual adult female survival explained the greatest amount of variation (62%) in lambda. Annual juvenile survival explained 44% of the variation in lambda, whereas summer or winter juvenile survival by themselves were far less informative. Winter fawn:doe ratios, a metric often collected by management agencies, explained only 10% of the variation in lambda. Given an adult female survival of 0.84, our simulations estimated a lambda of 1.0 (95% credible interval = 0.88–1.14), indicating equal probability that a population would increase or decrease. Simulations further indicated that given adult survival rates <70%, the population would always decline, but as survival increased lambda increased linearly. In contrast, estimates of lambda plateaued when annual juvenile survival reached approximately 0.5, indicating higher survival rates yielded diminishing

returns to population stability. Using simulated values within the observed range of vital rate values across the species' geographical distribution, the mean lambda was 0.975 and in 61% of the simulations, lambda was <1. After 20 years, we estimated that this distribution of lambda values would cause populations to decrease in 92% of instances with a mean decrease of 44%. Our results align with observed declines in mule deer populations throughout their range over recent decades and indicate that these trends will continue until management can improve survival of adult females.

KEYWORDS

large herbivore, life-stage simulation analysis, matrix model, *Odocoileus hemionus*, survival, ungulate

The application of matrix models to quantify animal population growth, and the associated perturbation analysis to understand the importance of individual vital rates to population growth, has underpinned many applications of wildlife population ecology and management in the last century. Lewis (1942) and Leslie (1945) first demonstrated that matrices could be populated with age-specific vital rates and that the dominant eigenvalue was equivalent to the long-term geometric growth rate (lambda or λ). Lefkovitch (1965) generalized the age-based (Leslie) matrix such that vital rates could be stage-based, and these Lefkovitch matrices have been important for organisms whose vital rates can easily be grouped into stage classes instead of the more restrictive data requirements of age-specific rates. Caswell (1978) was the first to apply perturbation analysis (i.e., sensitivity or elasticity analysis) to the dominant eigenvalue, demonstrating that different vital rates or different age or stage classes had variable contributions to lambda, with population growth being highly sensitive to certain vital rates but nearly invariant to others. For applied wildlife ecology, the method allowed for the evaluation of alternative management or conservation strategies by quantifying the expected overall effect on population growth rate *a priori*. Perhaps the most classic example of such perturbation analysis was the determination that turtle excluder devices, by protecting the age class with the highest sensitivity (large juveniles), would yield the greatest increase in population size when evaluating several management alternatives for loggerhead turtles (*Caretta caretta*) under a limited budget and high public scrutiny (Crowder et al. 1994).

While perturbation analysis is a powerful tool in applied wildlife management, it provides an incomplete understanding of how vital rates ultimately influence population growth because sensitivities and elasticities only quantify how lambda would be affected if vital rates changed, but they tell nothing about how they change, especially in the context of real systems. Failing to consider how much or little a vital rate has the potential to change has important implications when evaluating management alternatives because it would not be efficient to manage for the vital rate with the highest elasticity if that vital rate has almost no potential to vary in nature or in response to a management action. This is a common scenario confronting managers seeking to improve population performance because the evolution of life-history strategies has resulted in an inverse relationship between elasticity and variability in vital rates (Pfister 1998). Correspondingly, the vital rates with the greatest capacity to influence lambda are buffered the most from environmental variation and thus the least likely to change (Gaillard and Yoccoz 2003). Therefore, some combination of elasticity and variability within vital rates leads to certain ones explaining more variation in lambda than others. Although the difference between the elasticity of a vital rate to lambda versus the amount of variation it explains in lambda is subtle, the critical distinction is that elasticity alone describes the potential of the vital rate to influence lambda, whereas to understand the realized effect of a vital rate on lambda, one must instead focus on understanding how much variance in population growth can be explained by variation in the vital rate. Two analytical methods—lifetable response experiments (Caswell 1989) and life-stage simulation analysis (LSA;

Wisdom et al. 2000)—attempt to reconcile the difference between elasticity and the amount of variation a vital rate explains in lambda. Lifetable response experiments extend classical perturbation analysis to include variation in vital rates using analytical methods, whereas LSA uses simulations from probability distributions characterizing vital rates to evaluate lambda under a range of hypothetical scenarios to determine the influence of each vital rate on population growth. While both methods are useful, only LSA allows one to make probabilistic statements about population growth based on the influence of each vital rate as it varies with all other rates under defined probability distributions (Wisdom et al. 2000). In LSA, the amount of variation explained by a vital rate can easily be ascertained using the R^2 value from a linear regression that models lambda as a function of individual vital rates.

Large herbivores provide an ideal case study for employing LSA to understand the nuances between the potential ability for vital rates to influence lambda versus the realized ability for vital rates to influence lambda, particularly in natural systems occurring either through environmental variation or management actions. A strong body of literature supports the paradigm in which the life-history strategy of many large herbivores employs high and constant adult female survival but lower and more variable juvenile survival (Gaillard et al. 1998, 2000). Perturbation analysis consistently ranks adult female survival as having the highest elasticity (Gaillard and Yoccoz 2003), but in most systems it changes little because of selective forces buffering it from the effects of population density and environmental variation. As such, the prevailing dogma of large-herbivore life-history theory maintains that most of the interannual variation in population growth rate arises through variation in juvenile survival (Gaillard et al. 2000); however, the few studies to formally quantify this have not always agreed. For example, in an LSA for elk (*Cervus canadensis*), with vital rates compiled from populations across their North American distribution, Raithel et al. (2007) estimated that 75% of the variation in lambda could be explained by calf survival. However, in a more limited geographical extent in Montana, USA, calf survival explained <20% of the variation in lambda and adult female survival explained as much as 80% (Eacker et al. 2017), similar to the LSA results in a congener, the sika deer (*Cervus nippon*; Miura and Tokida 2009). In woodland caribou (*Rangifer tarandus caribou*), LSA determined that 54% of the variation in lambda was explained by adult survival and 43% by recruitment (DeCesare et al. 2012). In Sitka black-tailed deer (*Odocoileus heminous sitkensis*), lifetable response experiments revealed that adult female survival, by virtue of having almost no process error over the 3 years of a study in southeast Alaska, USA, contributed almost nothing to lambda despite it being the most elastic vital rate (Gilbert et al. 2020).

Mule deer (*Odocoileus hemionus*) and black-tailed deer (*Odocoileus hemionus columbianus*) are of high management concern in the twenty-first century because of declines from historical numbers; consequently, many state management agencies across the western United States have recently initiated large-scale demographic studies. As managers seek to reverse declining population trends, they will benefit from a thorough understanding of how age- or stage-specific vital rates ultimately contribute to population growth, and how certain vital rates may or may not be reliable predictors of lambda. While perturbation analyses specific to mule and black-tailed deer have demonstrated that they too display high elasticity to adult female survival (Bishop et al. 2009, Marescot et al. 2015, Gilbert et al. 2020, Lukacs and Nowak 2023), without proper consideration of both elasticity and variability, the degree to which adult female survival ultimately correlates with lambda cannot be fully understood. Local and regional studies have estimated process standard deviation (i.e., biological variation that is separate from sampling variation) surrounding adult female survival to be quite low (0.03–0.07; Unsworth et al. 1999, Lukacs et al. 2009), which indicates that the vital rate has evolved constancy and buffering from environmental variation. However, mean range-wide estimates of mule deer adult female survival (Forrester and Wittmer 2013) are lower than those of elk (Raithel et al. 2007), indicating that mule deer may have a greater capacity for adult survival to influence lambda given that a broader range of values could be attained (Sæther and Bakke 2000). Alternatively, mule deer have larger litter sizes and can reproduce earlier than elk, and the greater variation in reproductive output could plausibly cause fecundity to explain more variation in lambda than in elk.

Our objectives were to 1) conduct a range-wide literature review of mule and black-tailed deer vital rates, 2) use hierarchical models and Bayesian meta-analysis methods to characterize vital rates and correlations among vital rates using probability distributions, 3) employ LSA to determine the vital rates that explain the most variation in population growth, and 4) use output from the LSA to estimate the probability a population would increase given the observation of a point estimate of an individual vital rate. We hypothesized that similar to many other large

herbivores, population growth would be most influenced by variation in juvenile survival because it has the potential to vary greatly among years (Gaillard et al. 1998, 2000).

METHODS

Projection matrices

We first developed a stage-structured (Lefkovitch) model using a post-breeding, female-only matrix model to quantify mule deer population growth, classifying individuals into 3 stages: juveniles (age 0), yearlings (age 1), and adults (age ≥2). This model mirrors previous work by Bishop et al. (2009) and is identical to the matrix model described by Gilbert et al. (2020). This model assumes that yearling pregnancy, fecundity, and survival rates differ from those of adults but that all deer >2 years old have the same rates. In this initial model we favored simplicity over realism and did not assume senescence in reproductive or survival rates. The matrix is specified as follows:

$$\begin{bmatrix} 0 & P_y \times \frac{F_y}{2} \times S_y & P_a \times \frac{F_a}{2} \times S_a \\ S_j & 0 & 0 \\ 0 & S_y & S_a \end{bmatrix} \quad (1)$$

In this equation, P represents the annual pregnancy rate, F is litter size (number of offspring per parturient adult female), and S is survival. The subscripts denote different age classes, with j for juveniles, y for yearlings, and a for adults. Litter size is divided by 2 to assume an equal sex ratio of male and female fawns. We used the product of summer juvenile survival ($S_{j\,sum}$; 0–6 months) and winter survival ($S_{j\,win}$; 7–12 months) to estimate 12-month juvenile survival (S_j). In the modeling below, litter size is represented as the proportion of the parturient females that have twins. The derivation follows from the expression $(1 - p) \times 1 + p \times 2 = p + 1$, where p is the proportion of females that have twins and $(1 - p)$ is the proportion of females with single fawns. This approach allows twinning rate to be modeled on the logit scale, ensuring it stays within biologically feasible bounds of 0 and 1, similar to the other vital rates in the model. After modeling, we added 1 to the twinning rate to convert the value back to number of fawns per pregnant female. This approach assumes that a population's average litter size could not be >2, which is reasonable given that mule and black-tailed deer only rarely have triplets (Monteith et al. 2023).

The matrix described above has the beneficial qualities of being simple and composed of data commonly estimated and reported, allowing us to use nearly all the data from our literature review. However, it sacrificed realism with the assumption that all demographic rates of deer ≥2 years old are equal. While age-specific survival rates are less commonly reported than survival of broad age categories, the studies providing age-specific vital rates clearly demonstrate survival is reduced in older deer (Bishop et al. 2009, Monteith et al. 2014, Marescot et al. 2015). Evidence of senescence in reproductive parameters is much more ambiguous. Monteith et al. (2014) found that age did not influence pregnancy or litter sizes in a large sample of deer ≥2 years old, but other studies have found weak evidence of senescence in the same parameters (Bergman et al. 2014, Bender and Hoenes 2018, Hinton 2022). We thus included an age-structured (Leslie) model by constructing an additional matrix projection model that expanded Equation 1 to include age-specific survival and reproductive probabilities (Equation S1, available in Supporting Information).

Meta-analysis

We conducted a comprehensive literature review to characterize each vital rate in our matrices. We queried Google Scholar with all combinations of mule deer, black-tailed deer, or *Odocoileus hemionus* and vital rate, demographic rate, population dynamics, survival, reproduction, pregnancy, litter size, fecundity, and mortality.

We used only estimates in which a standard error associated with the point estimate was provided or in which we could derive one using the reported sample size or the 95% confidence interval. If a study did not provide a standard error but included a 95% confidence interval (CI), we imputed the standard error using $SE = \frac{(\text{upper CI} - \text{lower CI})}{3.92}$. In cases in which the 95% CI was provided only in a plot, we extracted the 95% CI bounds from the plot image using Graph Grabber 2.0.2 (Quintessa, Oxfordshire, United Kingdom; https://www.quintessa.org/software/downloads-and-demos/graph-grabber-2.0.2). If neither the standard error nor the 95% CI was provided but the sample size was reported, we used a beta-binomial model to estimate a standard error using the reported sample size as the number of trials and number of events (e.g., number surviving, pregnant) as the number of successes.

We used Bayesian logit-normal hierarchical models to estimate means, variances, and correlations among the vital rates in our matrix following Lukacs et al. (2009). It was important to use hierarchical models to isolate process variance from sampling variance and to accurately propagate uncertainty inherent in each study's vital rate estimates. A multivariate logit-normal distribution allows us to jointly model correlations among pairs of vital rates within a single model, capturing the mean and variance of each rate. However, to estimate correlations among all pairs of vital rates, each study would need to report all vital rates, which was not feasible. Most studies reported only one or several vital rates. To address this, we fit 2 sets of models. The first model set characterized the means and variances of each individual vital rate independently. The second model set estimated correlations among each pair of vital rates using a subset of the data.

For the first hierarchical model set, we used all available point estimates of each vital rate in Equation 1. The models were structured as follows:

$$\text{logit}(y_i) \sim \text{Normal}\left(\theta_i, \sigma_i^2\right) \tag{2}$$

$$\theta_i \sim \text{Normal}(\mu, \tau^2), \tag{3}$$

where y_i is observed vital rate from study i, θ_i is the true mean vital rate in study i on the logit scale, σ_i^2 is the within-study i variance (or sampling variance) of the logit-transformed vital rate, μ is the true, grand mean of the vital rate on the logit scale across studies, and τ^2 is the among-study variance (or process variance) of the logit-transformed vital rate. In other words, Equation 2 propagates uncertainty in each study's reported vital rate (y_i) by assuming the true vital rate varies around a mean θ_i with sampling variance σ_i^2 equal to the reported standard error of y_i. Equation 3 provides a biological description of the vital rate, wherein the range-wide mean vital rate on the logit scale is estimated by μ and the biological process error surrounding the mean is τ^2. Although parameters were logit-transformed, we only report results once back-transformed.

While $\text{logit}(y) = \log\left(\frac{y}{1-y}\right)$, to express a standard deviation of a variable y on the logit scale, one must use $\frac{\text{SD}(y)}{y \times (1-y)}$. Hence, in our study σ_i^2 for each study was specified as $\left(\frac{\text{SE}(y_i)}{y_i \times (1-y_i)}\right)^2$ where $\text{SE}(y_i)$ is the reported standard error of each study's vital rate estimate. The inverse logit can be used to back-transform parameters from the logit scale to the normal scale. For a vital rate μ on the logit scale, $\text{inverse logit}(\mu) = \frac{1}{1+\exp(-\mu)}$, and the variance surrounding μ (τ^2) can be back-transformed to the normal scale using $\tau^2 \times (\text{inverse logit}(\mu) \times (1 - \text{inverse logit}(\mu)))^2$.

The second set of models estimated correlations among studies that reported pairs of vital rates in (Equation 1) only, as it was immediately clear there would not be enough data to estimate correlations among all age-specific vital rates. These models were similar to the first set but assumed a bivariate normal distribution to estimate correlations:

$$\text{logit}(y_{i,j}) \sim \text{Normal}\left(\theta_{i,j}, \sigma_{i,j}^2\right) \tag{4}$$

$$\theta_{i,j} \sim \text{Bivariate Normal}(\boldsymbol{\mu}_j, \Sigma) \tag{5}$$

Here, i indexes the study and j indexes each pair of vital rates being jointly modeled, Σ is the covariance matrix, and all other parameters are as described above. The structure of Σ allows for the estimation of the variance of each vital rate and the estimation of the correlation between the 2 vital rates. Within Σ, diagonal entries represent process variance τ^2, and the subdiagonal elements represent covariances, which for a pair of vital rates is indicated by $\tau_1 \times \tau_2 \times \rho$, where ρ is the correlation coefficient between the 2 vital rates on the logit scale.

Consistent with findings by Forrester and Wittmer (2013), we observed that 12-month juvenile survival rates reported in studies were generally higher than rates derived by multiplying 0–6 month and 7–12 month survival values from studies providing seasonal estimates. To maximize data utilization and avoid potential bias, we estimated summer and winter juvenile survival rates from studies providing only 12-month survival estimates ($n = 48$). We achieved this by determining the relative contributions of summer and winter survival to annual survival and decomposing each 12-month estimate into seasonal components. Specifically, we realized that summer and winter survival rates could be derived from annual survival rates using $S_{j\,sum} = S_{j\,annual}{}^{x\_sum}$ and $S_{j\,win} = S_{j\,annual}{}^{x\_win}$, where $x_{sum} = \frac{\log(S_{j\,sum})}{\log(S_{j\,sum} \times S_{j\,win})}$ and $x_{win} = \frac{\log(S_{j\,win})}{\log(S_{j\,sum} \times S_{j\,win})}$. We then used the resulting $S_{j\,sum}$ and $S_{j\,win}$ estimates as data in the subsequent logit-normal models.

We used an Inverse Gamma(1, 1) prior for τ^2, a Normal(0, $\sigma^2 = 2$) prior for μ, and a Normal(0, $\sigma^2 = 4$) prior for ρ, truncated at −1, 1. We fit models using the nimble package (de Valpine et al. 2017) in Program R (R Core Team 2024) using 3 chains of 50,000 iterations, resulting in 150,000 posterior draws total after a 50,000 iteration burn-in phase. We ensured $\hat{R}$ values were <1.05 and visually inspected traceplots for convergence.

Life-stage simulation analysis

We conducted the LSA using the following approach. First, we simulated a random draw from a multivariate logit-normal distribution for each of the 150,000 posterior samples of the means, variances, and correlations (when possible) as estimated by the hierarchical models described above. This resulted in 2 datasets, both with 150,000 rows. The first dataset included values for each of 8 vital rates in the stage-structured matrix with the covariance structure as estimated from our meta-analysis. The second dataset contained values for each of the age-specific vital rates (44 total) in the age-structured matrix (Equation S1). The second dataset assumed vital rates were not correlated with one another. Second, for each of the 150,000 combinations of simulated vital rates in each of the 2 datasets, we populated a matrix (Equation 1 or Equation S1) and calculated the dominant eigenvalue as the expected population growth rate given that set of vital rate values. Finally, we used simple linear regression to model lambda (i.e., the dependent variable) as a function of each individual vital rate (i.e., predictor variables), and calculated the coefficient of determination (R^2) to determine the proportion of variance in lambda explained by each vital rate.

We also evaluated how well winter fawn:doe, or young-of-year:adult female, ratios could predict lambda because herd composition ratios are easily and often collected by wildlife managers. To do this we calculated what the expected fawn:doe ratio during winter would be for each set of simulated vital rates. We estimated the expected fawn:doe ratio for a given simulation by dividing the number of fawns produced per adult female that survived to be counted during winter herd composition surveys (the numerator) by the proportion of yearling and adult deer that survived until winter and could be counted during winter herd composition surveys (the denominator). Since only deer aged ≥2.5 years could have produced offspring (for a 1.5-year-old deer to have already produced a fawn, it would have had to become pregnant at age 0.5), the numerator counts fawns born to females aged ≥2.5 years. However, in the denominator, both yearling and adult females could be included as adult females when counted in herd composition surveys. The stable stage distribution (calculated from Equation 1) predicted that, over the long run, the population would be composed of 17% juveniles, 14% yearlings, and 67% adults ≥2 years. Taking the ratio of yearlings to adults ≥2 years old indicated 17% of the adult deer counted would be expected to be yearlings. Therefore, to account for the presence of yearlings in the denominator, we used a correction factor of 1.17.

Thus,

$$\text{winter fawn: doe ratio} = \frac{P_{adult} \times F_{adult} \times S_{juvenile\ summer}}{1.17 \times S_{adult\ summer}}, \quad (6)$$

where P is pregnancy rate, F is litter size, and S is survival. This equation required estimates of summer (~1 Jun–30 Nov) adult female survival, which were not available for the majority of studies we reviewed and therefore did not feature in our matrix model or simulations of correlated vital rates. Instead, we needed to scale each annual survival rate in our simulated dataset by a proportional value to reflect the fact that summer survival is measured over a shorter period than annual survival, and correspondingly the summer survival rates should be greater than annual survival rates. To make this adjustment, we recognized that $S_{summer} = S_{annual}{}^{x}$, wherein x is the scaling factor required to adjust annual survival to summer survival, and $x = \frac{\log(S_{summer})}{\log(S_{annual})}$. We estimated x by comparing reported summer and annual survival rates from 4 studies (Bender et al. 2007, Bishop et al. 2009, Hurley et al. 2011, Monteith et al. 2014). Then, we applied this scaling factor to predict a summer survival rate for each of the 150,000 simulated vital rates. We assumed yearlings and adults had similar summer survival rates so we did not separately calculate a summer survival rates for yearlings.

We then calculated analytical elasticity values for each vital rate to compare with the R^2 values. We used the popbio package (Stubben and Milligan 2007) in Program R to calculate elasticities.

Predicting population growth from key vital rates

We used the simulated vital rates to make probabilistic statements about lambda based on observed adult survival, juvenile survival, or winter fawn:doe ratios. We approached this in 2 ways. First, we plotted a line representing the proportion of simulations resulting in a population growth rate that was ≥1 for each value of key vital rates. This plot helped us visualize any nonlinear patterns in the relationships. For example, if a line plateaued, it would indicate diminishing returns–meaning that increasing the vital rate beyond a certain threshold would no longer appreciably improve the likelihood of population stability. Second, we plotted the mean and 2.5% and 97.5% quantiles of lambda as a function of vital rates. These plots are useful because if we observe a specific vital rate value, we can be 95% sure that population's growth rate will fall within the shaded region.

We summarized the values of lambda as estimated from 150,000 matrix model simulations to further assess how the vital rate combinations from our meta-analysis could plausibly influence populations. We first calculated the proportion of instances that resulted in a lambda <1 to describe the probability that the mean, range-wide vital rate estimates from our meta-analysis would result in a declining population. We then assessed how the distribution of lambda values observed in our simulations could plausibly influence populations over a 20-year period. To simulate population trajectories, we began with 10,000 populations each with an initial population size of 1,000 individuals (N_1 = 1,000) and iteratively updated N_{t+1} based on N_t and a randomly drawn value of lambda each year (λ_t) using $N_{t+1} = N_t \times \lambda_t$.

RESULTS

Meta-analysis

We used 72 data sources reporting 706 annual point estimates across 8 vital rates, plus an additional 16 point estimates for annual juvenile survival (i.e., without separate summer and winter juvenile survival estimates). Of the 72 data sources, 60 were conducted on mule deer, 11 on black-tailed deer, and 1 assumed hybrid black-tailed and mule deer population in their introgression zone. These studies represented 14 states and 2 Canadian provinces

with most studies conducted during the 2000s (Figure S1, available in Supporting Information). The most commonly reported vital rates were adult female survival and winter juvenile survival, and the least common were yearling survival and yearling litter size (Figure S2, available in Supporting Information).

The hierarchical logit-normal models fit to data from our literature review provided summaries of each vital rate in terms of its range-wide mean ($\bar{x}$) and process standard deviation (σ; Figure 1; Table 1). Summer (0–6 month) juvenile survival ($\bar{x} = 0.458$, $\sigma = 0.146$, $n = 52$) was lower but less variable than winter (7–12 month) survival ($\bar{x} = 0.613$, $\sigma = 0.224$, $n = 211$). Annual juvenile survival from studies reporting annual estimates of the vital rate ($\bar{x} = 0.308$, $\sigma = 0.130$, $n = 47$), were higher than the product of 0–6 month and 7–12 month fawn survival

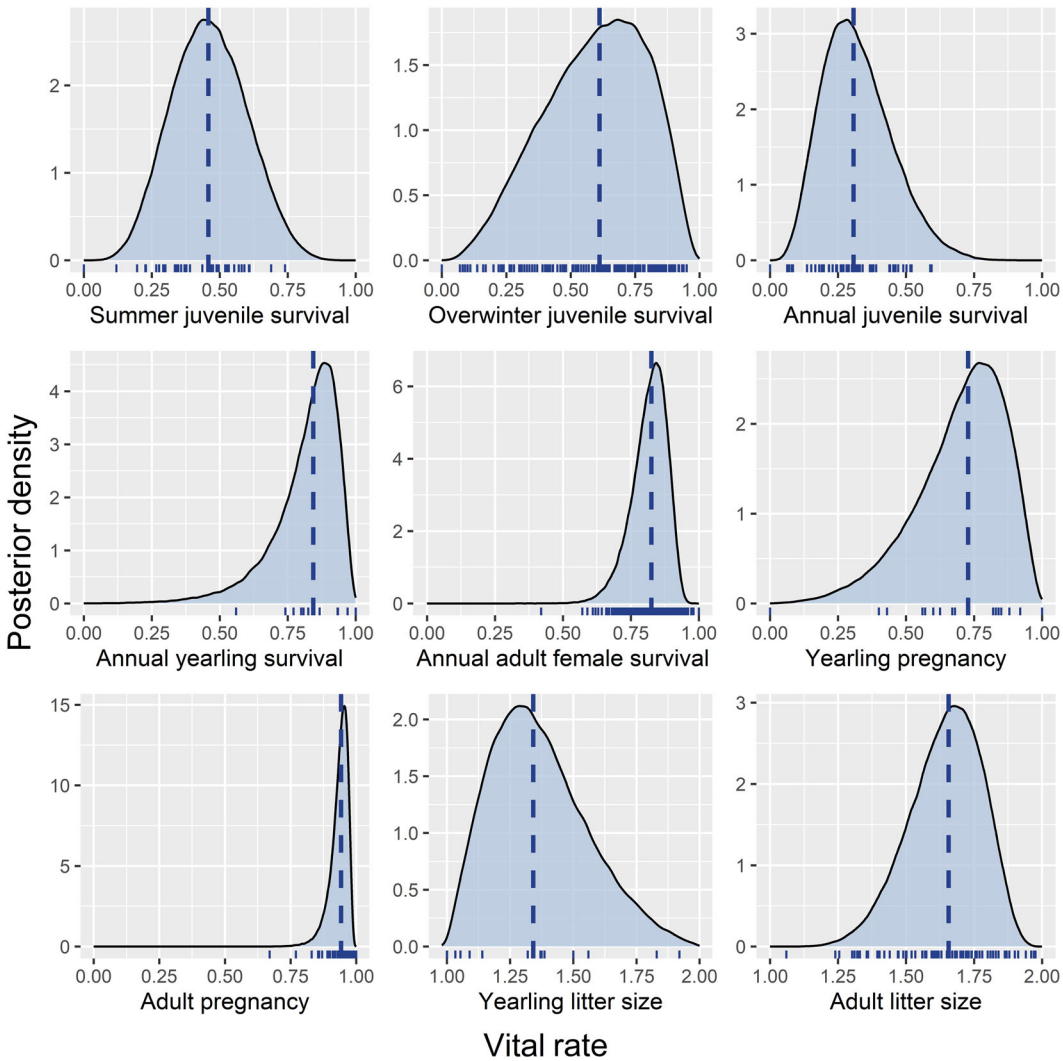

FIGURE 1 Posterior densities of mule deer vital rates fit using logit-normal hierarchical models summarized from a range-wide literature review. The vertical dotted line displays the posterior mean. The small vertical ticks on the *x*-axis show mean values of each point estimate used in the meta-analysis. Litter size refers to the number of offspring produced per pregnant female, and thus fecundity (number of offspring per adult female) is the product of pregnancy rate and litter size. Summer juvenile survival is from 0–6 months and winter juvenile survival is from 7–12 months of age.

TABLE 1 Summary of vital rates used in the life-stage simulation analysis for mule and black-tailed deer from a range-wide literature review and the number of point estimates (*n*; annual vital rates). Summer juvenile survival is from 0–6 months, and winter juvenile survival is from 7–12 months. We did not include studies reporting juvenile survival rates over shorter periods (e.g., 0–3 months).

Vital rate	Median	Mean	Process SD	*n*
Juvenile survival (annual)	0.308	0.308	0.130	47
Juvenile survival (summer)	0.458	0.458	0.146	52
Juvenile survival (winter)	0.613	0.613	0.224	211
Yearling survival (annual)	0.844	0.840	0.103	12
Adult female survival (annual)	0.826	0.826	0.063	249
Yearling pregnancy	0.728	0.726	0.161	22
Adult pregnancy	0.942	0.942	0.030	78
Yearling litter size	1.342	1.345	0.198	18
Adult litter size	1.657	1.657	0.138	96

probabilities (0.281). Annual yearling (1–2 yr) female survival ($\bar{x} = 0.840$, $\sigma = 0.103$) was similar but slightly higher and more variable than for adult (≥2 yr) females ($\bar{x} = 0.826$, $\sigma = 0.063$). The mean summer adult survival rate was 0.934. Yearling pregnancy ($\bar{x} = 0.726$, $\sigma = 0.161$) was substantially lower and more variable than adult pregnancy ($\bar{x} = 0.942$, $\sigma = 0.030$), whereas yearling litter size ($\bar{x} = 1.345$, $\sigma = 0.198$) was modestly lower than that of adults ($\bar{x} = 1.657$, $\sigma = 0.138$). The most variable vital rates were winter juvenile survival and yearling reproductive rates, whereas those with the highest precision were annual adult survival and adult pregnancy (Figure 2). Consideration of age-specific vital rates indicated that survival was highest among deer aged 3–5 and declined thereafter (Table S1, available in Supporting Information). Pregnancy rates and litter sizes in deer aged 2–7 were higher and less variable than for deer aged ≥8 years (Table S1).

Correlations (ρ) among vital rates could only be estimated for certain vital rates from studies with sufficient matched pairs (see non-NA entries in Figure 3; Table S2, available in Supporting Information), and of these, only 7 had Bayesian credible intervals that did not span 0 (colored entries in Figure 3; bold entries in Table S2). Summer and winter juvenile survival were the only vital rates that were negatively correlated ($\rho = -0.44$). Overwinter juvenile survival was positively correlated with both yearling and adult survival ($\rho = 0.79$ and $\rho = 0.23$, respectively), and adult survival also correlated positively with adult pregnancy ($\rho = 0.59$). Adult litter size was positively correlated with yearling pregnancy ($\rho = 0.70$), adult pregnancy ($\rho = 0.24$), and yearling litter size ($\rho = 0.74$). The remaining pairs of vital rates either could not be estimated because of insufficient data or had credible intervals that spanned 0.

Life-stage simulation analysis

The set of univariate regression analyses that treated lambda as the response variable and individual vital rates as predictors (Figure 4) revealed that the majority (62%) of variation in lambda was explained by adult female survival. Summer and winter juvenile survival explained 10% and 25% of the variation in lambda, respectively, yet annual juvenile survival (measured as the product of summer and winter juvenile survival) explained 44% of the variation in lambda. Yearling survival explained 22% of the variation in lambda, and yearling or adult pregnancy and litter size parameters explained <12% of the variation in lambda. We calculated expected winter fawn:doe ratios using

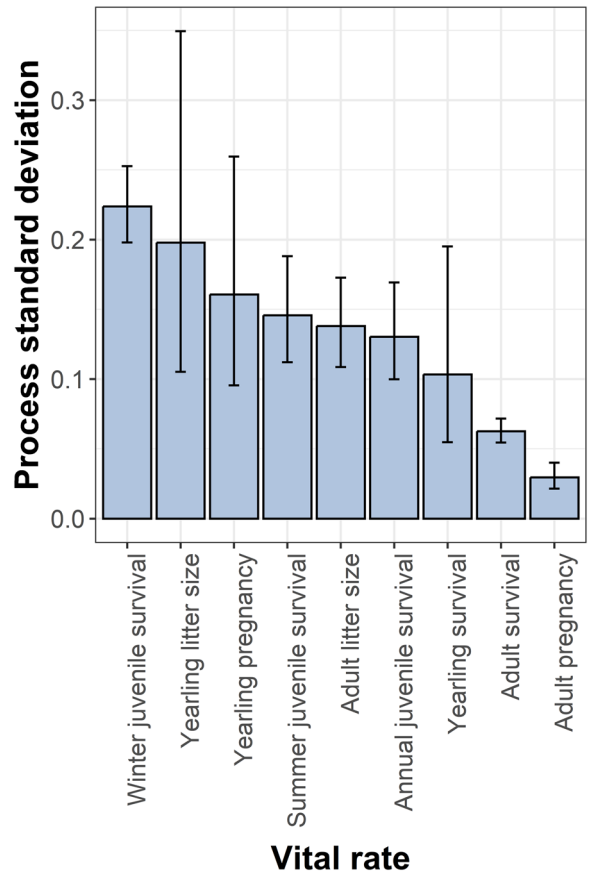

FIGURE 2 Estimates of process standard deviation (τ in Equation 3 on the normal scale) of mule and black-tailed deer vital rates, fit using logit-normal hierarchical models summarized from a range-wide literature review. Error bars represent 95% credible intervals for the estimate of the posterior standard deviation of the vital rate. Note that process standard deviation characterizes biological variability within vital rates and is separate from sampling variance.

Equation 6 and, as above, regressed it on lambda. The R^2 value from the regression indicated that winter fawn:doe ratios explained only 10% of the variation in population growth rate.

The age-specific LSA indicated that the survival of deer in the 2-year age class explained more variation in population growth than survival of any other age (Figure 5). Prime-aged deer (2–7 years) explained more variation in lambda than older adult deer (≥8 years) both in terms of survival and reproductive parameters (Figure 5).

Adult female survival was overwhelmingly the vital rate with the highest elasticity value (0.72) and was more than 5 times greater than the next most elastic vital rates at 0.14 (survival of juveniles during summer, overwinter survival of juveniles, and annual survival of yearlings; Figure 6). The terms constituting adult fecundity (pregnancy and litter size) had elasticity values slightly lower than juvenile and yearling survival (0.12), and the yearling fecundity terms were the least elastic with values of 0.02. Elasticity values and R^2 values from the LSA were similar among vital rates (Figure 6).

Predicting population growth from key vital rates

For a range of plausible values of key vital rates (juvenile survival, adult survival, and fawn:doe ratio), we calculated the proportion of instances in the simulated dataset that resulted in lambda values ≥1. For juvenile survival (either

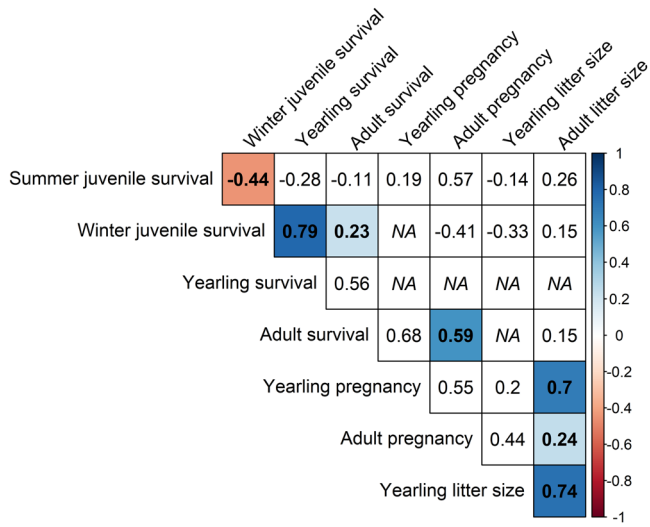

FIGURE 3 Estimates of the correlations (ρ) among pairs of mule and black-tailed deer vital rates fit using bivariate logit-normal hierarchical models summarized from a range-wide literature review. We use NA to represent pairs of vital rates with insufficient data to fit models. Colored entries represent correlations whose 95% Bayesian credible intervals do not overlap 0.

summer, winter, or annual) and fawn:doe ratios, the probability of observing a stable lambda began to plateau at high values of the vital rate (Figure 7). In contrast, the probability of observing a stable lambda continued to increase linearly even at high values adult female survival (Figure 7; Table S3, available in Supporting Information). In contrast to the juvenile survival rates, in which a stable lambda could be achieved across a wide range of values, there was almost no probability of observing a stable population when adult female survival was <0.7.

The vital rate values that predicted a stable population (i.e., a lambda of 1.0) were 0.84 for adult female survival (annual), 0.29 for annual juvenile survival, 0.48 for summer juvenile survival, and 0.62 for winter juvenile survival. By extension, higher or lower vital rate estimates would be indicative of increasing or decreasing populations, respectively. A winter fawn:doe ratio of 68:100 also predicted a stationary population (Figure 7).

The mean value of lambda across all 150,000 simulations was 0.975 ($\sigma = 0.11$), and 61% of these simulations indicated a lambda <1 (Figure 8). In our simulations that drew a random value from this distribution of lambda annually for 20 years, at the end of this period, 92% of simulations resulted in a population decline, with a mean decrease of 44%.

DISCUSSION

Our study suggests that mule and black-tailed deer deviate from the life-history paradigm intrinsic to many other large herbivores wherein most variation in population growth is attributed to the high variability of juvenile survival or recruitment. Instead, we demonstrate that adult female survival determines the majority of interannual variation in lambda by virtue of being lower and more variable in black-tailed and mule deer than in other ungulates yet still having a high elasticity. It is uncommon for LSA results in ungulates to point unequivocally to adult female survival as having the strongest contribution to population growth in addition to a high elasticity (but see DeCesare et al. [2012] and Eacker et al. [2017]). While summer and overwinter juvenile survival combined to explain 44% of the variation in lambda, annual adult survival explained 62% of the variation. In stark contrast, a similar range-wide analysis for elk demonstrated that 75% of the variation in lambda was explained by calf survival, and far less by

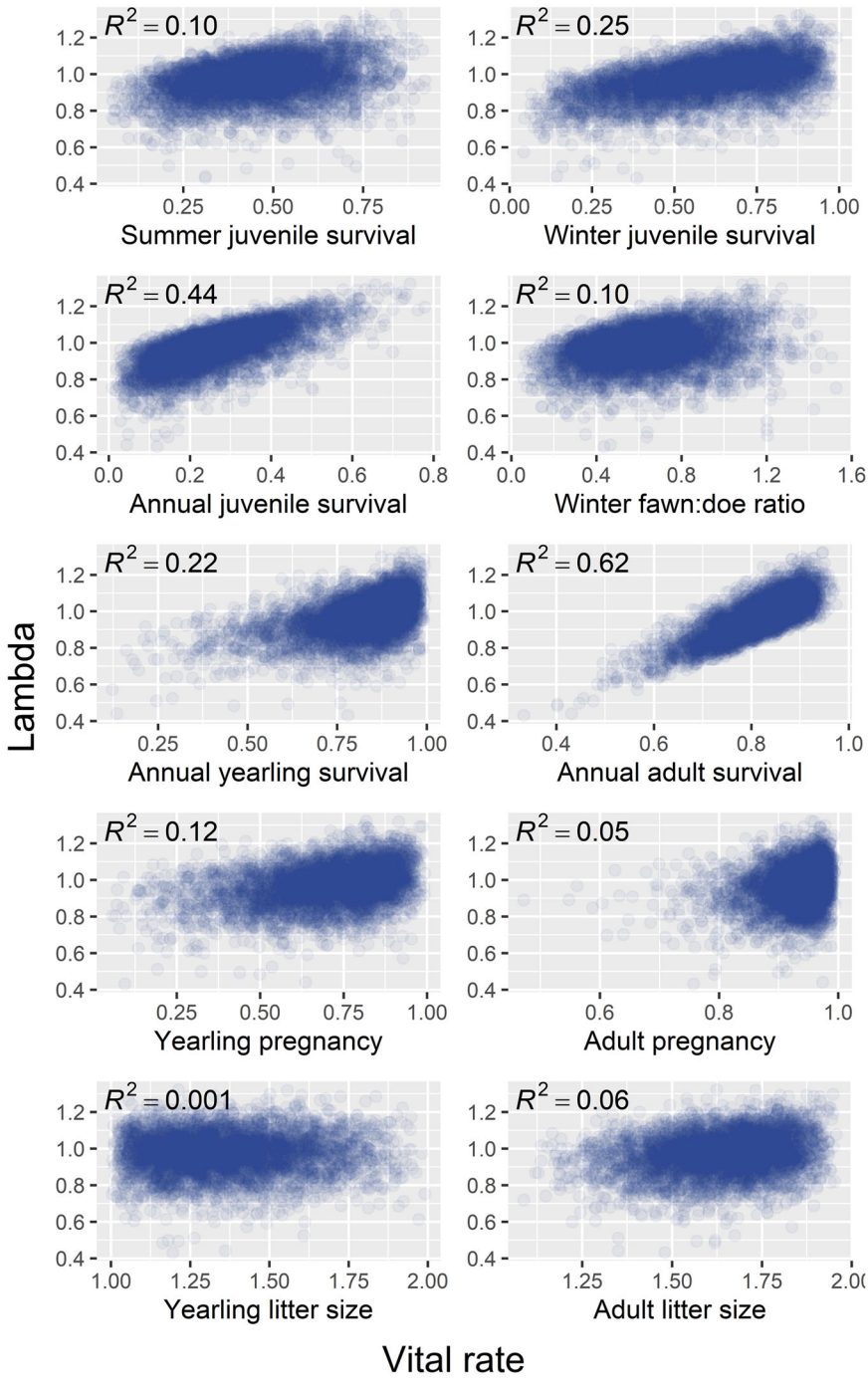

FIGURE 4 Results from life-stage simulation analysis on mule and black-tailed deer using vital rates summarized across their geographic distribution. Each scatterplot relates population growth (lambda) to an individual vital rate, wherein each datapoint reflects a random draw from a multivariate logit-normal probability distribution characterizing vital rates. We then used each set of randomly generated vital rates to populate a matrix model to calculate lambda. We used simple linear regression to model lambda as a function of each individual vital rate, and R^2 values measure the proportion of variation in lambda explained by each vital rate. In each plot, a random sample of 5,000 of the 50,000 simulated data points are plotted.

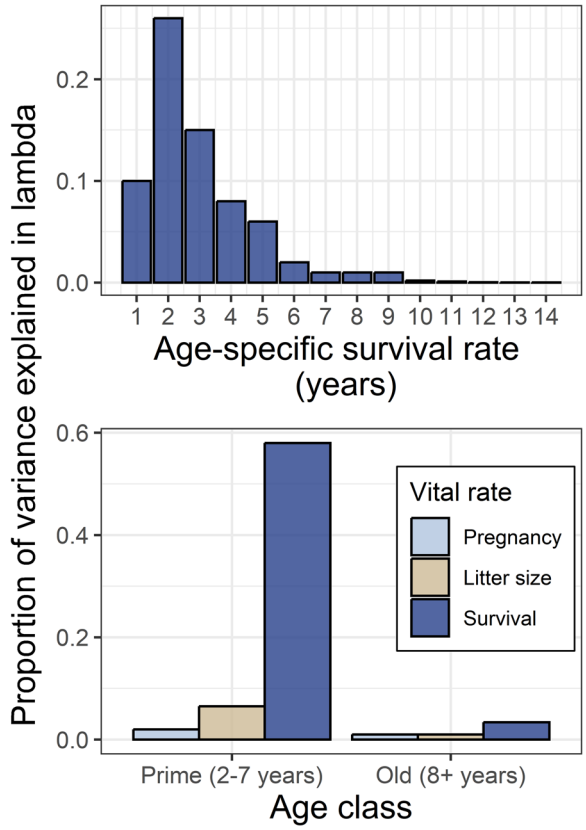

FIGURE 5 The proportion of variation explained (R^2 values from life-stage simulation analysis) in population growth rate (lambda) as a function of age-specific vital rates in black-tailed and mule deer from a range-wide literature review.

adult female survival (Raithel et al. 2007). Despite mule and black-tailed deer having a much greater reproductive capacity than elk because they can first breed as yearlings and produce larger litter sizes, fecundity contributed little to lambda both in terms of elasticity and predictive ability.

Our range-wide compilation of mule and black-tailed deer vital rates, which was needed to characterize the components of population growth for our simulations, generally agreed with the literature review by Forrester and Wittmer (2013). However, one difference was our estimation that adult female survival averaged 0.826, whereas that study estimated a mean of 0.84. While this difference in survival may seem trivial, our simulations suggest that this discrepancy could be the difference between a decreasing and stable population (lambda = 0.98 and 1.0, respectively). Although our meta-analysis used the same sources as Forrester and Wittmer (2013), our review added many additional studies that occurred during the last decade, which is probably the reason for the difference.

Correlations among vital rates suggested that most of the significant relationships between vital rates were positive. This pattern has been observed in other species of ungulates (Coulson et al. 2005, Lukacs et al. 2009) and other taxa (Sæther and Bakke 2000, Fay et al. 2022). One plausible explanation for the positive correlations in reproductive parameters that we observed is that in years with environmental conditions promoting a growing season favorable to deer, all reproductive parameters would benefit. However, this explanation is nuanced because there is substantial evidence demonstrating that reproductive rates in mule deer are high and invariant (Monteith et al. 2014, 2023) and only weak evidence that they are related to nutritional condition in adult deer. For example, although several studies report positive associations between body fat and pregnancy, the relationships had

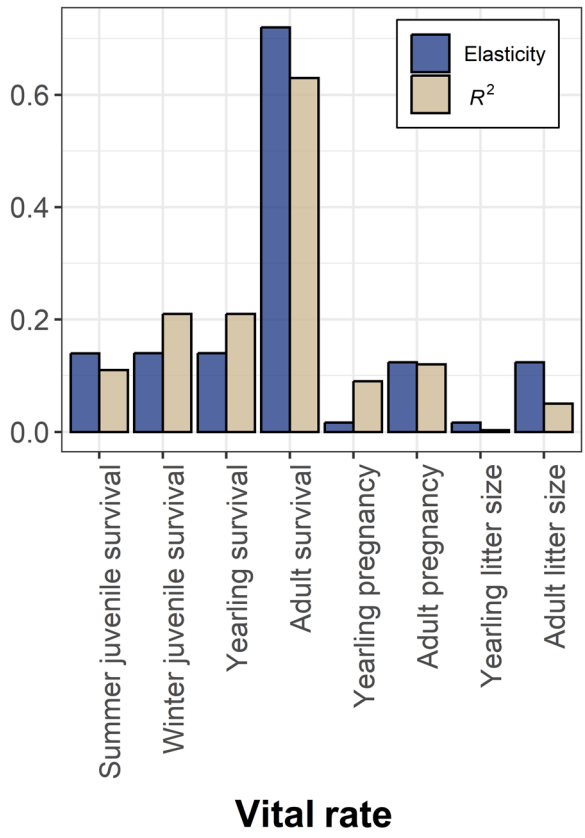

FIGURE 6 Comparisons of analytical elasticity values from a matrix population model and R^2 values from a life-stage simulation analysis in mule and black-tailed deer from a range-wide literature review. Elasticity values measure the magnitude of the change in lambda expected from a proportional change in a vital rate, and thus describe the potential ability for vital rates to influence population growth. R^2 values (coefficients of determination) in a life-stage simulation analysis measure the amount of variation in lambda that can be explained by individual vital rates under realistic scenarios, and thus describe the realized ability for vital rates to influence population growth.

confidence intervals that spanned 0 (Tollefson et al. 2010, LaSharr 2023) or were only identified in populations with extremely degraded range conditions (Julander et al. 1961). This probably owes to the fact that mule deer tend to rely more on nutritional intake (i.e., income) than body fat reserves (i.e., capital) for reproduction. Nutritional intake in summer and fall has thus been a stronger predictor of reproductive rates in mule deer than body reserves, with both high pregnancy and twinning rates positively associated with high dietary digestible energy intake rates (Tollefson et al. 2010). Thus, a positive correlation between pregnancy and litter size could be mediated by factors associated with interannual variation in availability of dietary digestible energy around the time of conception.

The reason for the positive correlation between adult pregnancy rate and survival is unclear given that these parameters are governed by different physiological measures. Deer generally use income (immediate energy intake) for pregnancy and capital (stored energy) for survival, and these energy sources are procured during different periods that are not necessarily related to each other (Kerby and Post 2013). Further, adult pregnancy and survival are the 2 most constant demographic rates in black-tailed and mule deer, with their relatively low variability making any explanation for their positive correlation difficult. Nonetheless, there may be rare instances under which extreme conditions act to reduce both survival and pregnancy. For example, for mule deer in stressful desert conditions, drought in summer or fall could potentially cause malnutrition that both increases mortality and decreases the income needed for conception

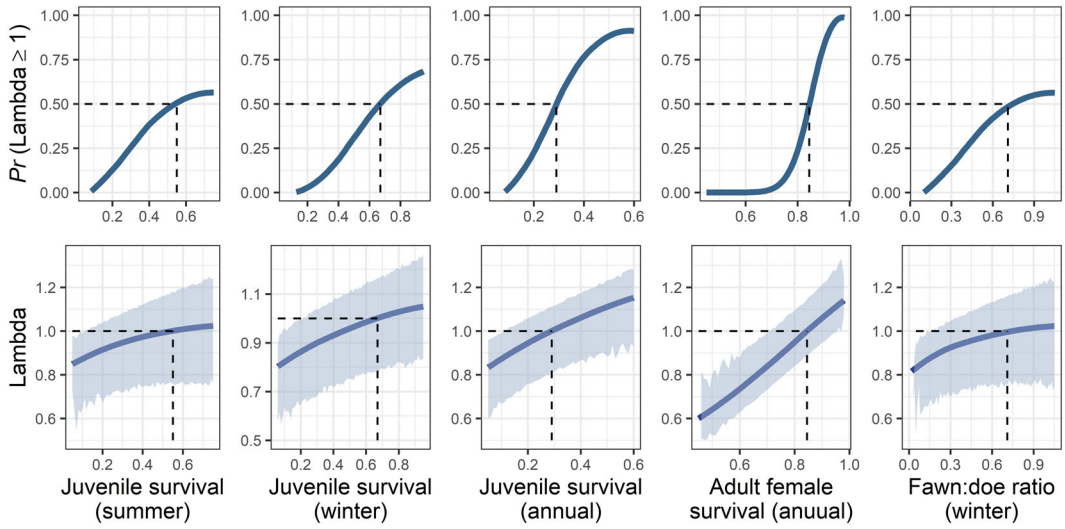

FIGURE 7 Output from life-stage simulation analysis in mule and black-tailed deer from a range-wide literature review used to make probabilistic statements regarding population growth given key life-history parameters. The top row quantifies the probability of observing a stable or increasing lambda given a single vital rate. The bottom row quantifies the expected value of lambda given a single vital rate, wherein the solid line displays the mean prediction of lambda, and the shaded band provides the 95% credible interval for lambda. The winter fawn:doe ratio was constructed from individual vital rates. X-axis values span the range of observed values for each vital rate. Dotted lines correspond to vital rate values predicted to result in a stable population.

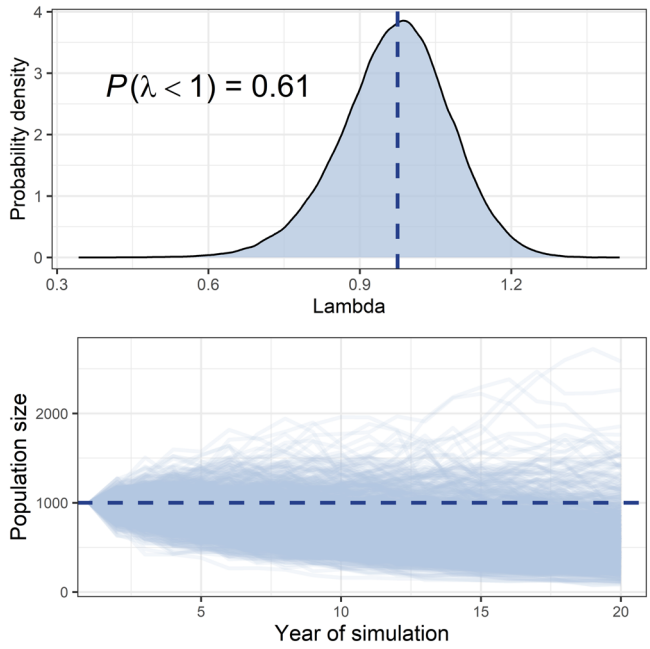

FIGURE 8 The distribution of lambda values as predicted from our matrix model simulations populated by range-wide estimates of mule and black-tailed deer vital rates (top). The dashed vertical line displays the mean of the distribution (λ = 0.975), and 61% of all simulated lambda values were <1. We also present simulations of 10,000 population trajectories over a period of 20 years, each with a starting population size of 1,000 (bottom). We simulated each population trajectory using randomly drawn values of lambda for each year. After 20 years, 92% of populations declined, with an average decrease of 44%.

(Bender and Hoenes 2018). The positive association we detected may have been driven largely by several outlying data points in terms of very low pregnancy and survival, with 2 such data points from populations in stressful desert environments (Lawrence et al. 2004, Bender et al. 2007; see Data File in Supporting Information). Populations limited by winter severity, however, may have very different correlations among adult survival and other reproductive parameters if they exhibit risk-sensitive reproductive allocation (Bårdsen et al. 2008, Monteith et al. 2013). Because large herbivores should forego reproduction to safeguard their own survival, a negative correlation between adult survival and reproductive measures might be expected in regions with severe winters if adult survival remains high but reproductive investment is reduced. Unfortunately, data limitations precluded assessment of differences in correlations between populations limited by severe winters versus populations not limited by winter conditions.

It was not surprising that overwinter juvenile survival positively correlated with both yearling and adult survival, and we similarly detected correlations between yearling and adult survival (although the latter was not significant). Summer juvenile survival did not correlate with annual adult survival, which was contrary to our expectations given that the death of an adult deer with dependent young would logically also result in the death of their neonates. But the fact that most adult mortality occurs in winter likely explains the lack of a relationship between adult survival and neonatal survival during the summer. An unexpected result was that summer and winter juvenile survival were negatively correlated. There are several reasons why summer and winter fawn survival could have an inverse relationship. First, if all fawns survived the summer, any winter mortality would mean winter survival would necessarily be lower and would lead to a negative correlation. Alternatively, if the smallest fawns all died in summer (Bishop et al. 2009, Hurley et al. 2011, Shallow et al. 2015), the sample surviving until winter should have a larger body mass and be better suited to survive. This conclusion is well supported by the effects of maternal condition on juvenile survival in mule deer (Bishop et al. 2009; Lamb et al. 2023; Monteith et al. 2014, 2023). This relationship also has implications for the effects of summer fawn predation on mule deer population growth. The largest reported cause of fawn mortality in the summer is predation (Forrester and Wittmer 2013). The relationship revealed in this study that low fawn survival in summer is associated with higher winter survival, along with results from predator removal studies that show no increase in mule deer population growth (Hurley et al. 2011, Forrester and Wittmer 2013), provides further evidence that summer fawn predation may be mostly compensatory. The negative correlation between summer and winter juvenile survival may also be mediated by weather where cold conditions during parturition may cause neonates to die from hypothermia (Linnell et al. 1995, Grovenburg et al. 2012), but these same conditions may be associated with longer access to nutritious forage in summer that would support good body condition entering winter (Pettorelli et al. 2007). Nonetheless, situations where reproduction or fawn survival is reduced likely stem from nutritional issues (Bishop et al. 2009, Monteith et al. 2014). In that case, habitat improvement projects will likely provide the greatest benefit to the population.

While the LSA based on the stage- and age-structured matrix projection models produced qualitatively similar results, in that survival of adults was far more explanatory than juvenile survival or any reproductive rate, the results from the age-structured analyses were illuminating. The fact that 26% of the variation in population growth could be explained by the survival of 2-year-old deer alone demonstrates the importance of young adult deer. In contrast, survival rates of deer >6 years old contributed almost nothing to lambda. This is notable because preferentially focusing resources on managing for higher survival of younger adults instead of older deer, to the extent possible, would likely show a greater response in the population. If there are sources of mortality that are indiscriminate across age classes (such as vehicle collisions), and other sources of mortality that are biased toward older deer (such as mortality from some predators), then the potential for mortality to be additive for certain sources should be considered. Future studies should investigate whether mortality sources are substantially different between younger and older adult deer.

As part of the LSA, we populated matrix models 150,000 times using plausible vital rate values, which allowed us to predict both lambda and the probability of observing a growing population as a function of individual vital rate values. Although we hoped a single vital rate could precisely forecast population growth, we observed substantial uncertainty in lambda estimates from even the vital rates with the greatest predictive ability. For example, when adult female survival was 84%, we predicted lambda would be 1.0, though with a 95% credible interval of 0.88–1.14.

A more definitive finding was that an adult female survival rate ≤0.7 would cause populations of mule or black-tailed deer to decrease with near certainty, even if other vital rates were high. While survival rates <0.7 are rare given that adult female survival should be buffered from environmental variation (Gaillard and Yoccoz 2003), we found 18 point estimates of adult survival below this value in our literature review. Our estimation that, on average, a winter fawn:doe ratio of 68:100 would be needed to observe a stable population was similar to the estimate of 66:100 by Unsworth et al. (1999). Winter fawn:doe ratios explained only 10% of the variation in lambda and a stable population could be observed across nearly all plausible values of fawn:doe ratios, indicating limited utility for using these ratios for monitoring or forecasting population trends. For example, if 68 young per 100 adult females were observed on winter range, we would predict a stable population that year, but with 95% confidence we would have to assume that lambda could be anywhere between 0.74 and 1.16, a range so wide it is not useful. Intuitively, young:adult female ratios will only accurately index recruitment when the denominator, adult female survival, is high and constant, which we show is not always the case. That said, fawn:doe ratios can still provide a useful input to integrated population models currently employed by many wildlife management agencies when other parameters are also included. For example, if adult female survival and young:adult female ratios are both included in an integrated population model, it would be possible to solve for parameters not directly measured, such as neonatal survival.

The range-wide average vital rates for mule and black-tailed deer predicted a lambda of 0.975, or a 2.5% decline per year, which is not a positive sign for the species. Further, only 8% of our simulations of population trajectories based on plausible lambda values were indicative of an increasing population over a 20-year period, with the remaining predicting an average decrease of 44% during that time. We caution, however, that this assessment could appear overly bleak if the studies reporting vital rates that formed the basis of our analysis were somehow biased low. Should poorly performing populations be allocated more resources for study by state wildlife agencies, a reporting bias may occur. However, our results are broadly consistent with observed declining trends in black-tailed and mule deer across their range (Jensen et al. 2023). For example, of 11 states and provinces reporting estimates of black-tailed and mule deer population estimates between 2000 and 2020 (Jensen et al. 2023), only 17% reported population increases over that time, with an estimated regional population decline of 25%. Of course, our simulation results are useful only if past conditions mirror those of the future (Wisdom et al. 2000). Not all mule and black-tailed deer populations are currently experiencing declines, and further studies should investigate the factors and vital rates associated with stable and increasing populations. Our findings indicate that whether or not mule and black-tailed deer populations will increase or decline will in large part be determined by future adult female survival rates.

MANAGEMENT IMPLICATIONS

Managers often focus on mule deer life stages of reproduction or juvenile survival, but our results indicate the strong need to monitor and manage adult female survival because it explains the majority of variation in population growth. Moreover, even small changes in adult female survival result in disproportionately large changes in population growth relative to improvement of other vital rates. In areas with declining mule deer populations, managers should investigate adult female survival rates to determine if they are likely to produce a declining population (i.e., survival below 84%) and if so, use cause-specific mortality evidence to guide management actions. Monitoring adult survival can be done through use of satellite collars or similar technologies, in which a large number of adult females should be monitored to ensure that the parameter is measured with high precision. Management can likewise focus on a wide range of factors to improve adult female survival in a holistic manner including reduction of antlerless tags (which could be a logical first step), improvements in nutrition and other habitat factors, increased surveillance of illegal harvest, preservation of migration corridors, and mitigation of vehicle-caused mortality on roads and highways, all of which must be considered within the context of changing climatic conditions and recovering large carnivore populations. In populations in which adult female survival is sufficiently high (e.g., >84%) but populations remain below expectations, managers should then investigate other vital rates (e.g., fawn survival and reproduction) to determine if they are responsible for reduced population performance.

In situations where reproduction or fawn survival is reduced, it is likely related to nutritional issues (Bishop et al. 2009, Monteith et al. 2014) and habitat improvement projects will likely provide the greatest benefit to the population.

Our probability-based estimates of population growth and associated uncertainty provided by credible intervals allow managers to carefully interpret their monitoring estimates of adult female survival or any other vital-rate estimates in relation to population growth, and to evaluate how well management improvements may result in desired changes in population growth or trends. Given the range-wide, long-term declines in populations of mule deer, more holistic approaches to monitoring and management of adult survival are needed to inform and implement best management practices for recovery.

CONFLICTS OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

This study used data from the literature only. Readers should refer to the original studies for animal use and care protocols.

DATA AVAILABILITY STATEMENT

The data used in this manuscript are the result of a literature review, and all data and their sources are included in the Supporting Information.

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Associate Editor: Kevin Monteith.

SUPPORTING INFORMATION

Additional supporting material may be found in the online version of this article at the publisher's website.

How to cite this article: Ruprecht, J., T. D. Forrester, D. A. Clark, M. J. Wisdom, J. B. Smith, and T. Levi. 2025. Variability and correlations among vital rates and their influence on population growth in mule and black-tailed deer. Journal of Wildlife Management 89:e22690. https://doi.org/10.1002/jwmg.22690