Demographic vital rates and population growth: rethinking the relationship in a harvested elk population

Jonathan M. Conard[1] and Philip S. Gipson[2]

[1]Natural Science Department, Sterling College, Sterling, KS 67579

[2]Department of Natural Resources Management, Texas Tech University, Lubbock, TX 79409

US Army CERL

Nature Precedings : doi:10.1038/npre.2009.3609.1 : Posted 14 Aug 2009

Introduction

For long-lived vertebrates, adult survival is generally the vital rate with the highest stage-specific elasticity (e_{ij}) value. However, adult survival is relatively invariant in response to changes in environmental conditions or population density (Gaillard et al. 1998, Pfister 1998, Gaillard et al. 2000, Eberhardt 2002). Recent findings suggest that vital rates with high variability may be more important for determining the actual rate of population change ( ) than invariant vital rates with higher elasticity values (Pfister 1998, Wisdom et al. 2000, Raithel et al. 2007).

For harvested populations, variation in harvest regulations, hunter access, and success rates could increase variability in adult survival. Similarly, small populations may experience increased variability in vital rates due to demographic stochasticity. Therefore, it is important to determine if the relationship between observed vital rates and rates of population change in small/harvested populations is consistent with the hypothesis that adult survival rates in ungulates are relatively invariant when compared to other vital rates (Gaillard et al. 1998, Gaillard et al. 2000), and that variability in juvenile survival has a greater influence on λ than adult survival (Raithel et al. 2007).

Methods

•We studied a harvested elk population at Fort Riley Military Reservation, Kansas

•We captured 34 female elk and monitored survival using radio-telemetry from October 2003 – February 2007. During capture, we removed a tooth for aging, drew blood for pregnancy testing, determined lactation status, and measured subcutaneous body fat levels using ultrasonography.

•We used the 'nest survival' model in Program MARK to estimate annual adult survival rates and model environmental and individual covariates related to survival. We estimated annual rates of calf survival based on autumn lactation and pregnancy rates. We estimated fecundity (female offspring / female / year) based on pregnancy rates and assumed a 1:1 sex ratio at birth.

•We parameterized a matrix model based on a life-cycle with vital rates including fecundity (F), calf survival (S_o), yearling survival ($S_{yearling}$), prime-age adult survival (2-9 years old) (S_{prime}), old-age survival (10+ years old) (S_{old}), and a stage-transition probability ( ) (Fig. 1).

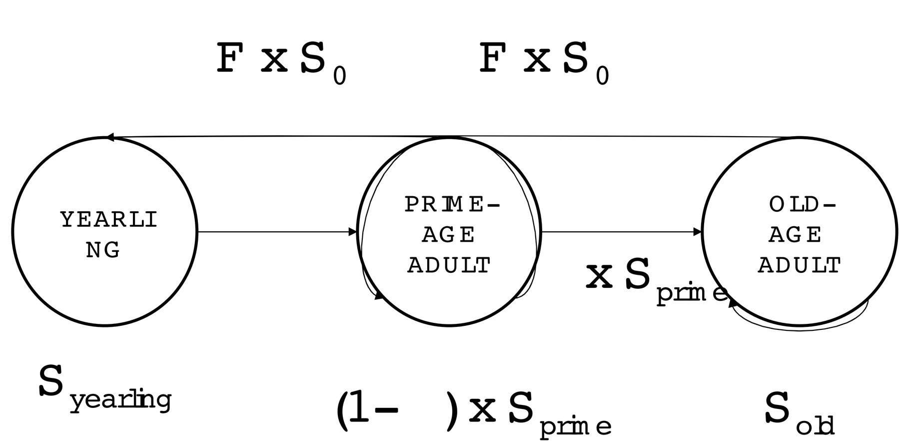

Fig. 1. Life-cycle diagram for matrix model

•We used life-stage simulation analysis (LSA) to simulate the relationship between population growth rate ( ) and underlying demographic vital rates. We conducted LSA based on repeated matrix projections, with values for each vital rate drawn from a uniform distribution encompassing the range of values observed for that vital rate.

Results

•Eight mortalities occurred during the study as a result of hunting (6), wounding (1), and other (1) causes.

•The overall annual adult survival rate was 0.76 (var($\hat{S}_{overall}$) = 0.005), with higher estimates of survival for 2004-2005 ($\hat{S}_{2004\text{-}2005}$ = 0.83, var($\hat{S}_{2004\text{-}2005}$) = 0.012) and 2005-2006 ($\hat{S}_{2005\text{-}2006}$ = 0.89, var($\hat{S}_{2005\text{-}2006}$) = 0.01). Model-averaged monthly survival estimates were higher during non-hunting season months (April-September) (Fig. 2).

•Age was the only covariate included in the best-supported model (AIC = 0), and was negatively related to adult survival (= -0.18).

•Overall calf survival was 0.73, and annual estimates ranged from 0.57 (2005) to 1.0 (2007).

•Fecundity was generally high, with an overall estimate of 0.48.

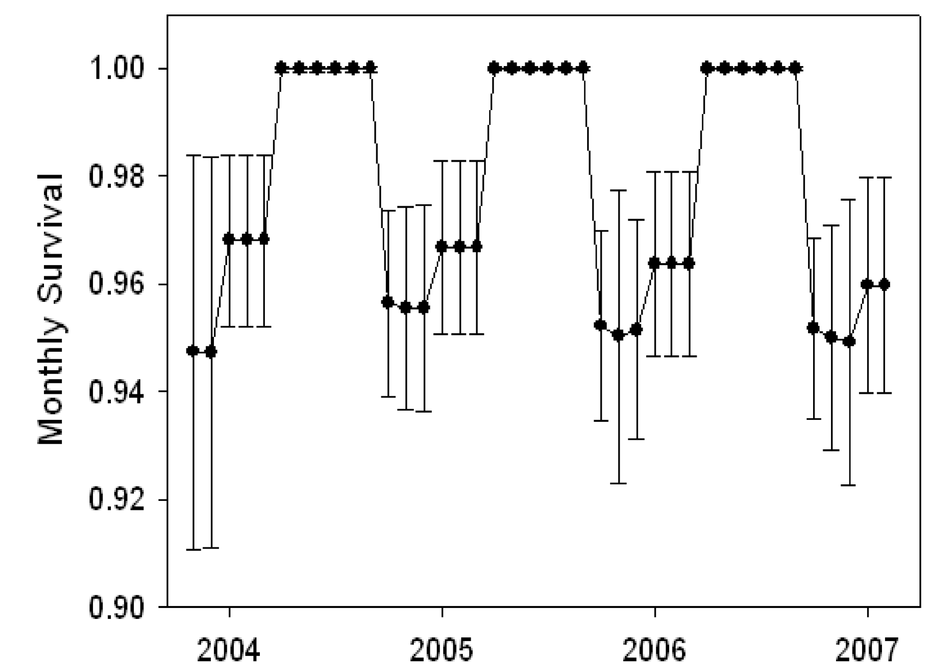

Fig. 2. Monthly adult female survival rates for an elk population at Fort Riley, Kansas.

•Based on deterministic matrix model projections from observed vital rates, we predicted the elk population at Fort Riley to have a slightly positive overall rate of population change (λ = 1.033).

•Summed elasticities were highest for prime-age adult survival matrix elements (0.49), followed by yearling survival (0.24), and prime-age recruitment (0.21) (Fig. 3).

Cow elk mortality at Fort Riley, Kansas

E =
0 0.21
0.24 0.46 0
0 0.03
0.03
0.02

Fig. 3. Matrix of estimated elasticity values

•Life-stage simulation analysis results indicated that the greatest amount of variation in λ was explained by variation in calf survival (r^2 = 0.606) and prime-age adult survival (r^2 = 0.367).

•Other vital rates including yearling survival (r^2 = 0.002), old-age survival (r^2 = 0.006), prime-age fecundity (r^2 = 0.004), and old-age fecundity (r^2 = <0.001) explained little of the observed variation in λ.

Discussion

Life-history theory suggests that vital rates with high elasticity values should exhibit reduced levels of variation in response to environmental variability (Pfister 1998). This hypothesis has been supported based on findings of high elasticity coupled with low temporal variability in adult survival rates and low elasticity coupled with high temporal variability for juvenile survival rates in ungulates (Gaillard et al. 1998, Gaillard et al. 2000, Raithel et al. 2007).

Cow elk at Fort Riley, Kansas

Variation in adult elk survival rates were explained primarily by age, with older age-class adults having lower survival rates. Similar results have been found for cervid populations with large predators present (Kunkel and Pletscher 1999) where older individuals may be more susceptible to predation than prime-age adults (Wright et al. 2006). Our results suggest that previous findings of age-dependence in adult survival for ungulates (Gaillard et al. 2000, Festa-Bianchet et al. 2003) are supported for a population where harvest is the primary source of mortality.

High elasticity values for prime-age adult and yearling survival rates suggest that changes in these vital rates will have a large influence on λ. This finding is not unexpected, as survival is generally recognized as the vital rate with the highest level of elasticity for long-lived species (Eberhardt 2002).

Results from life-stage simulation analysis (LSA) generally supported the hypothesis that calf survival has a greater realized influence on λ than adult survival. However, it is important to note that the variability in λ explained by adult survival in the small, harvested Fort Riley population (r^2 = 0.367) was several times greater than that reported over a range of elk populations (r^2 = 0.164) (Raithel et al. 2007). These findings suggest that further work may be necessary to determine how population size and harvest status influence the relative variability of adult and calf survival rates and the realized influence of these vital rates on λ.

Literature Cited

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

Gaillard, J-M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology and Evolution 13:58-63.

Festa-Bianchet, M., J-M. Gaillard, and S. D. Cote. 2003. Variable age structure and apparent density dependence in survival of adult ungulates. Journal of Animal Ecology 72:640-649.

Gaillard, J. M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toigo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31:367-393.

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

Pfister, C. A. 1998. Patterns of variance in stage-structured populations: evolutionary predictions and ecological implications. Proceedings of the National Academy of Science 95:213-218.

Raithel, J. D., M. J. Kauffman, and D. H. Pletscher. 2007. Impact of spatial and temporal variation in calf survival on the growth of elk populations. Journal of Wildlife Management 71:795-803.