Sensitivity analysis as a guide for population management of pronghorn

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Abstract: Sensitivity analysis can be a valuable tool for management and conservation of declining pronghorn populations. Calculation of elasticities is a type of sensitivity analysis which measures proportional effect of vital rates on the finite rate of increase (λ). We calculated elasticity associated with each age-specific vital rate over 500 replicates of a leslie matrix population model. Vital rates were chosen randomly for each replicate within predetermined bounds derived from empirical life table data. Fawn survival was associated with the highest elasticity in all 500 replicates. Yearling and 2-yr old survival had the second and third highest elasticities, respectively. For all age classes, survival was associated with higher relative elasticity than reproductive rate. The results of this analysis support the hypothesis that fawn survival is the most important factor affecting λ of pronghorn populations.

KEY WORDS: Elasticity, Leslie matrix, pronghorn, sensitivity analysis, survival, reproduction.

INTRODUCTION

Pronghorn (*Antilocapra americana*) range across much of western North America, but current populations are scattered and fragmented (Byers 1997). Although some populations have stabilized, others continued to decline (Yoakum 1978). To guide conservation efforts, managers can benefit from knowing which life stages or vital rates have the greatest effect on population growth. Several studies used sensitivity analyses to investigate the relative importance of age- or stage-specific vital rates (Maguire et al. 1995, Schmutz et al. 1997, Wisdom and Mills 1997) to changes in the finite rate of increase (λ).

Sensitivity analysis can be used to calculate the elasticity of λ associated with each vital rate (Caswell 1989, Wisdom and Mills 1997). Elasticities are proportional sensitivities which can take values between 0 and 1. By considering the proportional effects of vital rates on λ, individual components of a population matrix sum to 1, making comparison among different types of vital rates possible (de Kroon et al. 1986). This approach can identify age-classes

and vital rates which should be targeted by managers to affect population growth most effectively. Using a Leslie matrix approach, we test the hypothesis that fawn survival will have a larger effect on ? than adult survival or fertility.

METHODS

Parameter Estimation

We used data from the literature to estimate pronghorn age-specific survival and reproduction. To encompass the range of possible values, we selected the highest and lowest estimate available for each vital rate. Age-specific survival (S_x) was obtained from life table data compiled by Byers (unpublished data) and Mitchell (1980) from a total of four populations. We defined S_x as the finite rate of survival during the age interval x to x+1, where S_x = $(n_x-d_x)/n_x$. Although reports of age-specific adult S_x in the literature were limited, estimates of fawn survival were more abundant (Ellis 1972, Pyrah 1976, Beale 1978, Vriend and Barret 1978, Neff and Woolsey 1980). However, as a large proportion of fawn mortality occurs within the first few weeks after birth (Barrett 1978, Autenrieth 1980), we did not use estimates of fawn mortality based on mid-summer surveys. Only fawn counts conducted within a few days of birth provide accurate measures of early post-natal fawn survival.

Reproductive effort in ungulates is generally high (Case 1978, Robbins 1993), and may reach an extreme in pronghorn (Byers and Moodie 1990). Byers (1997) found that fecundity of pronghorn on the National Bison Range in Montana is invariant, with all females producing twins each year. Studies of other populations reported fawning rates as low as 1.8 - 1.9 fawns/adult female (Ellis 1972, Beale 1978). We defined age-specific reproduction (R_x) as the number of female fawns/female/year. Since considerable data suggest a 1:1 sex ratio in pronghorn (Edwards 1958, Pyrah 1976, Mitchell 1980, Byers 1997), we obtained R_x by multiplying the total number of fawns/female by 0.5.

To establish the upper and lower bounds of vital rates, we used the highest and lowest estimates available from the literature (Table 1). After defining the bounds of R_x and S_x, We used these values to parameterize the elements of age-specific fertility (F_i) and survival (P_i) in a Leslie matrix population model (Table 2). Wisdom and Mills (1997) recommended this procedure to evaluate elasticity over a realistic range of vital rates.

Model description.

To determine elasticities of each vital rate, we used ELASTIC6, a DOS-based program written by L. S. Mills. Parameter estimates from the literature were used to specify the upper and lower bounds on vital rates, incorporating possible variation between populations and environmental conditions (Table 1). Randomly selected values from within the specified bounds were parameterized in a post-birth pulse Leslie matrix model (Caswell 1989, Wisdom and Mills 1997). The top row matrix elements contained age-specific fertilities (Fi), which were

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Table 1. Demographic components, range of values, associated vital rates and Leslie matrix elements used to calculate elasticities of lambda for pronghorn. Low and high values were used to establish the bounds of vital rates, and to parameterize the elements of age-specific fertility (F_i) and survival (P_i) in a Leslie matrix population model.

Demographic component	Range of values (source)	Vital rate	Matrix element
Number of female Fawns/ female/year[a]	0.9 (Beale 1978) to 1.0 (Byers 1997)	R_1 through R_{15}	F_1 through F_{15}
Fawn (age 0) survival	0.113[a] to 0.326[b]	S_0	P_0, F_0[c]
Adult (age 1) survival	0.409[b] to 1.0[a]	S_1	P_1, F_1
Adult (age 2) survival	0.968[a] to 1.0[b]	S_2	P_2, F_2
Adult (age 3) survival	0.447[b] to 0.967[a]	S_3	P_3, F_3
Adult (age 4) survival	0.617[b] to 1.0[a]	S_4	P_4, F_4
Adult (age 5) survival	0.460[b] to 0.957[a]	S_5	P_5, F_5
Adult (age 6) survival	0.327[b] to 0.952[a]	S_6	P_6, F_6
Adult (age 7) survival	0.727[b] to 0.971[a]	S_7	P_7, F_7
Adult (age 8) survival	0.320[b] to 0.936[a]	S_8	P_8, F_8
Adult (age 9) survival	0.200[b] to 0.958[a]	S_9	P_9, F_9
Adult (age 10) survival	0.0[b] to 1.0[a]	S_{10}	P_{10}, F_{10}
Adult (age 11) survival	0.0[b] to 0.786[a]	S_{11}	P_{11}, F_{11}
Adult (age 12) survival	0.0[b] to 0.857[a]	S_{12}	P_{12}, F_{12}
Adult (age 13) survival	0.0[b] to 0.600[a]	S_{13}	P_{13}, F_{13}

[a] J. Byers, unpublished data.
[b] Mitchell 1980:141-142.
[c] Fawn reproduction assumed to be zero (Byers 1997), thus F_0 was also assumed to be zero.

calculated as the product of $(R_x)(S_{x-1})$. The off-diagonal matrix elements equaled female probability of surviving the previous time step (P_i). We generated 500 replicates, with each composed of a different set of randomly selected vital rates from within the given range. For each replicate, ? was calculated, and the mean elasticities associated with each vital rate among the replicates were determined. Vital rates associated with the highest elasticity values represented the rates with the largest effects on ?.

Table 2. Estimates of the lower (a) and upper (b) bounds on age-specific fertility (Fi) and survival (Pi) for pronghorn. Estimates are organized in a post-birth pulse Leslie matrix, with Fi along the top row and Pi down the sub-diagonal. Lower-bound matrix (a) contains values of 0 for columns 11-15.

a

0	0.368	0.871	0.402	0.555	0.414	0.294	0.654	0.288	0.180
0.113	0	0	0	0	0	0	0	0	0
0	0.409	0	0	0	0	0	0	0	0
0	0	0.968	0	0	0	0	0	0	0
0	0	0	0.447	0	0	0	0	0	0
0	0	0	0	0.617	0	0	0	0	0
0	0	0	0	0	0.460	0	0	0	0
0	0	0	0	0	0	0.327	0	0	0
0	0	0	0	0	0	0	0.727	0	0
0	0	0	0	0	0	0	0	0.320	0
0	0	0	0	0	0	0	0	0	0.200
0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0

b

0	1.000	1.000	0.967	1.000	0.957	0.952	0.971	0.936	0.958	1.000	0.786	0.857	0.600	0.330
0.326	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	1.000	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	1.000	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0.967	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	1.000	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0.957	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0.952	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0.971	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0.936	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0.958	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	1.000	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0.786	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0.857	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0.600	0

RESULTS

Fawn survival (S_0) showed the highest elasticity across the range of vital rates (Figure 1), and had the highest elasticity for all 500 replicates. Age-specific survival (S_x) had consistently higher associated elasticities than did age-specific reproduction (R_x) for every age-class (Figure 1). The second-highest elasticity was associated with yearling survival (S_1), and the third-highest elasticity was associated with 2-yr old survival (S_2). Relative ranking of the three highest elasticities was consistent for all 500 replicates. The distribution and range of λ showed these elasticities were applicable across variable population growth rates (Figure 2).
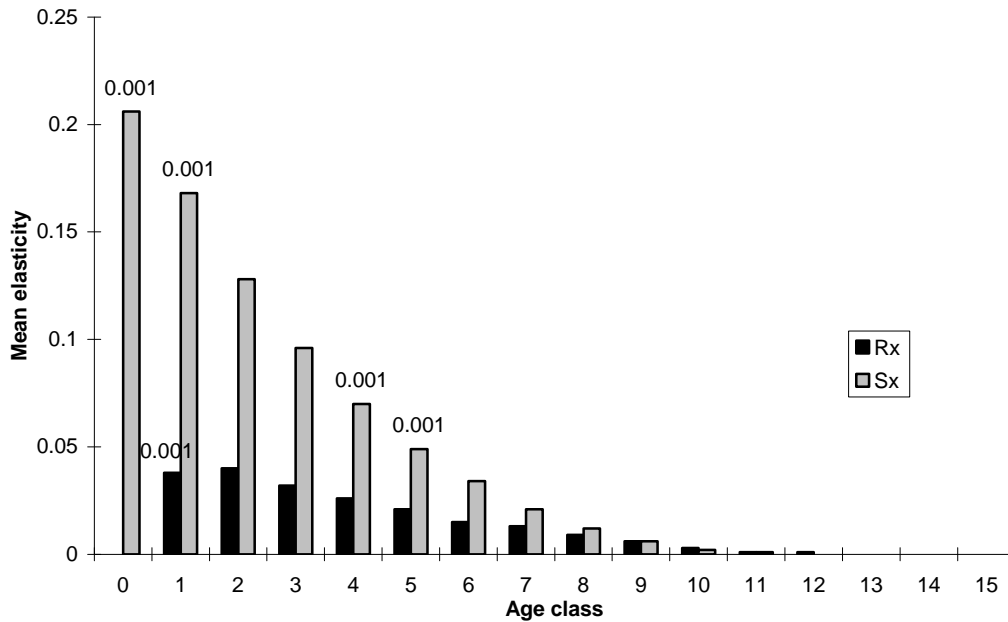

Figure 1. Mean Elasticities of age-specific survival (Sx) and reproduction (Rx) for pronghorn calculated from 500 replicates of a Leslie matrix population model. Shown with all SE values that were > .0001.
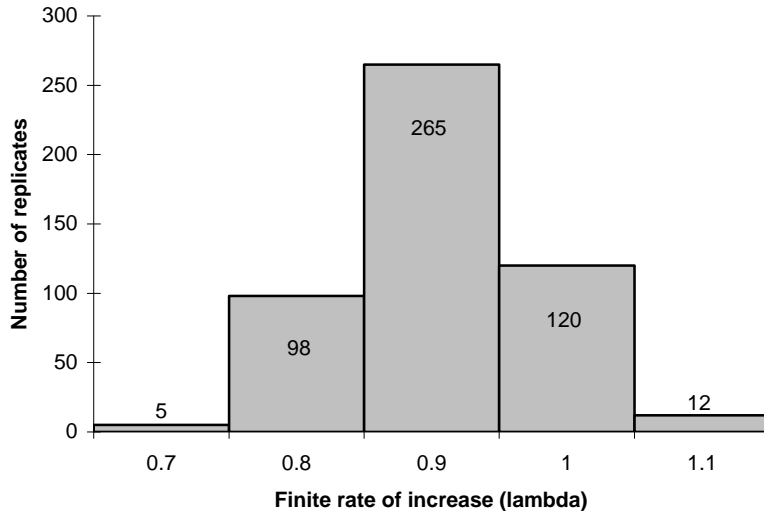
Figure 2. Distribution and range of the finite rate of increase (lambda) for pronghorn based on 500 replicates of a Leslie matrix population model

DISCUSSION

To promote the recovery and stability of pronghorn populations, managers can benefit from knowing how changes in survival and reproduction would affect λ. The results of our sensitivity analysis suggest that fawn survival is the most important factor contributing to changes in λ, followed by yearling and 2-yr old survival. The importance of fawn survival and recruitment has been emphasized in the literature (Vriend and Barrett 1978). The majority of fawn mortality is typically due to predation by coyotes, bobcats, and golden eagles, and predator control effected pronghorn population increases in multiple cases (Barrett 1978, O'Gara and Malcolm 1988, Byers 1997).

In addition to fawn survival, yearling and 2-yr old survival rates were associated with relatively high elasticities. These results may reflect the large potential variance in adult survival due to hunter harvest. The lowest estimates of S_1 and S_2 were obtained from a hunted population (Mitchell 1980). In hunted populations, reduction of early age-class-harvest combined with predator control would be the most effective way to increase population growth. Low elasticities associated with older age classes ($S_{x\geq6}$) suggest that harvest of older individuals would not significantly affect λ.

Before changing management plans to incorporate the results of elasticity analysis, it is important to consider the underlying assumption that vital rates are measured accurately (Schmutz et al 1997). In our analysis of pronghorn, the range of possible vital rates may have been underestimated due to scarcity of demographic data. In particular, fecundities of pronghorn under poor environmental conditions are not known, but are currently under investigation (M. Robinson, pers. comm). With accurate estimation of vital rates, sensitivity analysis is a valuable tool for managers that can guide allocation of future management and research efforts.

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