
Using Logistic Regression to Analyze the Sensitivity of PVA Models: a Comparison of Methods Based on African Wild Dog Models

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Abstract: *We used logistic regression as a method of sensitivity analysis for a stochastic population viability analysis model of African wild dogs (*Lycaon pictus*) and compared these results with conventional sensitivity analyses of stochastic and deterministic models. Standardized coefficients from the logistic regression analyses indicated that pup survival explained the most variability in the probability of extinction, regardless of whether or not the model incorporated density dependence. Adult survival and the standard deviation of pup survival were the next most important parameters in density-dependent simulations, whereas the severity and probability of catastrophe were more important during density-independent simulations. The inclusion of density dependence decreased the probability of extinction, but neither the abruptness nor the inclusion of density dependence were important model parameters. Results of both relative sensitivity analyses that altered each parameter by 10% of its range and life-stage-simulation analyses of deterministic matrix models supported the logistic regression results, indicating that pup survival and its variation were more important than other parameters. But both conventional sensitivity analysis of the stochastic model which changed each parameter by 10% of its mean value and elasticity analyses indicated that adult survival was more important than pup survival. We evaluated the advantages and disadvantages of using logistic regression to analyze the sensitivity of stochastic population viability models and conclude that it is a powerful method because it can address interactions among input parameters and can incorporate the range of parameter variability, although the standardized regression coefficients are not comparable between studies. Model structure, method of analysis, and parameter uncertainty affect the conclusions of sensitivity analyses. Therefore, rigorous model exploration and analysis should be conducted to understand model behavior and management implications.*

Utilización de la Regresión Logística para Analizar la Sensibilidad de Modelos de AVP: una Comparación de Métodos Basados en Modelos de Perros Silvestres Africanos

Resumen: *Utilizamos la regresión logística como un método de análisis de sensibilidad par a un modelo de análisis de viabilidad poblacional de perros silvestres Africanos (*Lycaon pictus*) y comparamos estos resultados con análisis de sensibilidad convencionales de modelos estocásticos y determinísticos. Coeficientes estandarizados de los análisis de regresión logística indicaron que la supervivencia de cachorros explicaba la mayor variabilidad en la probabilidad de extinción, independientemente de que el modelo incorporara la denso-dependencia. La supervivencia de adultos y la desviación estándar de la supervivencia de cachorros fueron los parámetros que siguieron en importancia en simulaciones de denso-dependencia, mientras que la severidad y la probabilidad de catástrofes fueron más importantes durante simulaciones denso-independientes. La inclusión de la denso dependencia disminuyó la probabilidad de extinción, pero ni la severidad ni*

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la inclusión de denso-dependencia fueron parámetros importantes. Resultados de los análisis de sensibilidad relativa que alteraron cada parámetro en 10% de su rango y análisis de la simulación de etapas de vida de modelos matriciales determinísticos apoyaron los resultados de la regresión logística, indicando que la supervivencia de cachorros y su variación fueron más importantes que otros parámetros. Sin embargo, el análisis de sensibilidad convencional del modelo estocástico que cambiaron cada parámetro en 10% de su valor medio y el análisis de elasticidad indicaron que la supervivencia de adultos fue más importante que la supervivencia de cachorros. Evaluamos las ventajas y desventajas de utilizar la regresión logística para analizar la sensibilidad de modelos estocásticos de viabilidad poblacional y concluimos que es un método poderoso porque puede atender interacciones entre parámetros ingresados e incorporar el rango de variabilidad de parámetros, aunque los coeficientes de regresión estandarizada no son comparables entre estudios. La estructura del modelo, el método de análisis y la incertidumbre en los parámetros afectan las conclusiones del análisis de sensibilidad. Por lo tanto, se debe realizar una rigurosa exploración y análisis del modelo para entender su comportamiento y sus implicaciones en el manejo.

Introduction

Population viability analysis (PVA) typically involves the creation of mathematical models to evaluate the risk of extinction over specified time intervals, the rate of population growth, or some related measure of population health (Beissinger & Westphal 1998; Beissinger & McCullough 2002). Sensitivity analyses are often used to examine the dynamics of PVA models. By quantifying the degree that changes in parameter values affect model outcomes, sensitivity analyses can determine which model inputs most affect model outcomes and may identify the management strategies likely to be most effective for species recovery.

The most frequent form of sensitivity analysis for deterministic models of population growth using stage or age-based matrices is elasticity analysis (e.g., Crouse et al. 1987; de Kroon et al. 2000). Elasticities quantify the proportional change in population growth rate (λ) from an infinitesimal proportional change in that vital rate and indicate which vital rate has the greatest effect on λ (de Kroon et al. 1986; Caswell 2000a, 2000b). Elasticity analyses address relative changes in vital rates (Table 1), so they are used to compare the influence of rates measured on different scales (e.g., fecundity and survival). This method depends on the estimates of vital rates used in the matrix (Caswell 1996) and rarely incorporates variability in vital rates (but see Grant & Benton 2000). Conclusions based on elasticity analyses may change depending on parameter values (Silvertown et al. 1996; Mills et al. 1999; Wisdom et al. 2000). Wisdom and Mills (1997) and Wisdom et al. (2000) suggest the use of life-stage simulation analysis (LSA) to explore how sensitivity relates to the entire range of variability in a vital rate. In LSA, random sets of matrices are first constructed by the drawing of vital rates from specified probability distributions bounded within the observed range of the rate. Each matrix is then analyzed to calculate λ , elasticity, or other matrix attributes. Finally, correlations be-

tween the matrix attributes and the vital rates used in the matrices are calculated to determine which vital rate explains the most variation (Table 1). Life-stage simulation analysis has been called a “retrospective analysis” because it depends on the magnitude of past variation in vital rates, whereas elasticity has been categorized as a “prospective analysis” because it projects how future change in a vital rate will effect population growth (Horvitz et al. 1997; Caswell 2000a, 2000b), even though it uses past averages of vital rates. There are additional approaches, such as life-table response experiments, which have specific applications for analyzing the elasticity and sensitivity of matrix models (Ehrlén & van Groenendael 1998; Caswell 2000a; Grant & Benton 2000). We do not address them here because they are not appropriate for the objectives of this study, although they may be useful in other PVA applications.

Sensitivity analyses of stochastic PVA models, which yield probabilistic estimates for the rate of extinction or other model outcomes, are not possible with the analytical techniques discussed above for deterministic matrix models. The conventional method of sensitivity analysis for stochastic PVA models is to determine the change in the probability of extinction related to a change in a model parameter by a fixed percentage (Armbruster & Lande 1993; Beissinger 1995). This method involves adjusting model parameters one at a time, conducting many iterations of the model for each new parameter set, and comparing the results with the average outcome, which is calculated by setting all input parameters to their mean value (Table 1). We refer to this approach as the conventional method of sensitivity analysis. This method, like elasticity analysis, does not incorporate variability in parameter estimates and would be considered a prospective approach (*sensu* Caswell 2000b). When these methods are used to evaluate management strategies, however, it is assumed that all parameters are equally variable and equally able to be manipulated. An alternative approach to analyzing the sensitivity of stochastic PVA models is to

Table 1. Summary of different sensitivity methods used and their characteristics.

| Method ^x | Model ^a | Perturbation ^b | | | Dependent variable ^c | Metric ^d | Interpretation | Source ^e |
|--------------------------|--------------------|---------------------------|------------|--------|---------------------------------|---------------------|--|---------------------|
| | | \bar{x} | σ^2 | type | | | | |
| Lower-level elasticity | D | yes | no | fixed | λ | e | effect of infinitesimal, proportional change | 1 |
| Life-stage simulation | D | no | yes | random | λ | r^2 | variation (%) explained by vital rate | 2 |
| Conventional sensitivity | S | yes | yes | fixed | extinction (%) | ΔE | effect of fixed change in parameter mean | 3 |
| Relative sensitivity | S | yes | yes | fixed | extinction (%) | ΔE | effect of fixed change in parameter mean scaled by parameter range | 4 |
| Logistic regression | S | yes | yes | random | extinction (%) | α/SE | relative importance scaled by uncertainty | 5 |

^aType of model: D, deterministic stage-based matrix model; S, stochastic population viability analysis model (run in VORTEX).

^bIndicates whether perturbed mean (\bar{x}), variance of input parameters (σ^2), and parameter values (type) varied by a fixed percentage or a random process.

^cModel output evaluated by sensitivity analysis.

^dMetric produced by sensitivity analysis used to evaluate effect of input parameters on dependent variable: e , elasticity coefficient; r^2 , coefficient of determination; ΔE , percent change in the rate of extinction; α/SE , standardized regression coefficient.

^eSources: 1, de Kroon et al. (1986); 2, Wisdom & Mills 1997; 3, Armbruster & Lande 1993; 4, this paper; 5, McCarthy et al. 1995.

change each variable by a fixed percentage proportional to the range of each variable. This allows one to evaluate proportional change that is scaled by the magnitude of the potential for change. We refer to this approach as the relative method of sensitivity analysis because it explores the effects of changes in parameter values relative to the variability of each parameter (Table 1). It has both retrospective and prospective elements because it evaluates the prospect of specific future changes based on past variation. For both conventional and relative methods, interactions of multiple parameters are difficult to address because there are many possible parameter combinations. In addition, neither method accounts for nonlinear relationships, such as the effect that adult sex ratio may have on the probability of extinction (McCarthy et al. 1995).

McCarthy et al. (1995, 1996) pioneered the use of an alternative approach, logistic regression, to analyze the sensitivity of stochastic PVA models. They used a stochastic PVA model to generate population sizes after a simulated time span for many different sets of input parameter values. Then the model output was converted to a binary variable (e.g., extinction or persistence) and used in a logistic regression with model input parameters as independent variables (Table 1). The relative importance of each input parameter was indicated by the value of its standardized regression coefficient. Like LSA, logistic regression could be considered a retrospective approach to sensitivity because it uses past variability in vital rates (Caswell 2000b). Logistic regression can address interaction terms, covariation of independent variables, and a range of parameter values. In addition, polynomials may be used to account for nonlinear relationships (McCarthy et al. 1995). Despite the apparent advantages of using logistic regression to evaluate the sensitivity of stochastic PVA models, the approach of McCarthy et al. (1995, 1996) has received little attention, and logistic regression remains a relatively unused method of analyzing sensitivity.

We evaluated logistic regression as a method of sensitivity analysis for stochastic PVA using a well-known model of African wild dogs (*Lycoan pictus*). Historically, wild dogs ranged across most of sub-Saharan Africa, but their populations have declined greatly over the past 30 years (Woodroffe & Ginsberg 1998). Recently, only six populations were believed to support >100 individuals (Woodroffe et al. 1997). Causes of decline include habitat loss, persecution by humans, competition with other large carnivores, and outbreaks of disease (Ginsberg et al. 1995a, 1995b; Creel & Creel 1996, 1998; Woodroffe et al. 1997; Woodroffe & Ginsberg 1998). In 1992, Burrows et al. suggested that the extinction of wild dogs in the Serengeti was due to the stress caused by invasive research methods. This hypothesis generated controversy (Burrows 1992; Burrows et al. 1994; Gascoyne & Laurenson 1994; Burrows et al. 1995; Ginsberg et al. 1995a, 1995b; Kat & Alexander 1995; de Villiers et al. 1995; East 1996; East & Hofer 1996; East et al. 1997; Woodroffe et al. 1997). To determine the likely cause of extinction, a PVA was conducted with the program VORTEX (Lacy 1993). Using the conventional method of sensitivity analysis, Burrows et al. (1994) found that disease outbreaks are important model parameters and concluded that the Serengeti population of wild dogs is unlikely to go extinct in the absence of disease outbreaks. Using virtually the same model, parameter values, and method of sensitivity analysis as Burrows et al. (1994), Ginsberg et al. (1995b) determined that carrying capacity and density dependence were the important model parameters. They concluded that the Serengeti population was likely to go extinct by chance. These different conclusions were due partly to different assumptions about density dependence and to incomplete sensitivity analyses of the two models. Recent wild dog models have also explored the importance of interspecific competition, social organization, and home-range size on extinction dynamics (Woodroffe & Ginsberg 1998; Vucetich & Creel 1999).

A better understanding of wild dog population dynamics and the causes of extinction might have emerged had more rigorous sensitivity analyses been undertaken to investigate the role of alternative model structures and sensitivity methods. We used the same stochastic PVA model reconstructed in VORTEX, and simpler deterministic models, to compare the results of different sensitivity analyses and to investigate some aspects of African wild dog population dynamics. Our goal was not to develop the most accurate or complete description of wild dog population dynamics to estimate the risk of extinction. Instead, our objectives were (1) to explore the efficacy of logistic regression for analyzing the sensitivity of stochastic PVA models and (2) to see to what degree management decisions based on sensitivity analysis are affected by different methods of analysis. We assessed logistic regression as a method of sensitivity analysis by comparing the results with conventional and relative methods of sensitivity analysis. To investigate the generality of our conclusions, we compared these results with sensitivity analyses based on simpler deterministic matrix models for the wild dog which used the same vital rates and model structure that we used in the stochastic PVA model. Deterministic matrix models have fewer variables and are less realistic, but they provide the underlying structure of more complex, stochastic PVA models because the rate of extinction rate is highly influenced by population trends (i.e., λ).

Methods

Reconstructing the Stochastic PVA Model in VORTEX

We used VORTEX 8.03 (Lacy 1993) to reconstruct previous stochastic models of wild dog population dynamics (Burrows et al. 1994; Ginsberg et al. 1995b) as closely as possible. Because our goal was to recreate the previous models and not to produce more accurate estimates of the risk of extinction, we did not attempt to develop better estimates of vital rates or to correct the estimates of variance in vital rates by removing sampling variance (Gould & Nichols 1998; White et al., unpublished data).

To address the conflicting results of Burrows et al. (1994) and Ginsberg et al. (1995b) caused by the presence or absence of density dependence in the model, we constructed both density-dependent and density-independent models. Half the VORTEX simulations included density dependence, which is modeled in VORTEX with the equation

$$B_N = B_0[1 - (N/K)^\beta] + B_K(N/K)^\beta,$$

where B_N is the percentage of females breeding at population size N , B_0 is the maximum percent breeding when the population size is zero, B_K is the minimum percent

breeding at carrying capacity K , and β dictates the shape of the density-dependent function (Lacy 1993). This equation is an extension of the logistic growth equation, except that it operates on the percentage of females that breed, it has a minimum value of B_K instead of zero, and it uses an "abruptness" parameter, β . When $\beta = 1$, the density-dependent function is linear from the maximum to the minimum percentage of females breeding. As β increases, density dependence becomes more curvilinear, and its effect is delayed. In our analysis, β varied from 1 to 50. The other half of the VORTEX simulations were density independent and included a carrying-capacity term that acted as a reflective ceiling to population size. To be consistent with previous wild dog models, we did not consider Allee effects or inbreeding depression.

Parameter values for the VORTEX simulations (Table 2) were taken from the models of Burrows et al. (1994) and Ginsberg et al. (1995b) and augmented from the wild dog literature. The minimum and maximum percentage of females breeding were determined by making the conservative assumption that only one adult female bred per pack (Fuller et al. 1992; Burrows et al. 1994, 1995). Burrows et al. (1994) estimated there were 1.7–2.7 adult females per pack, so the percentage of females breeding may range from 37% to 59%. We chose a slightly larger range of 35–60%. Age at first reproduction was 2 years, and mating was monogamous. Burrows et al. (1994) estimated the litter size of Serengeti wild dogs ranged from 9 to 10.4. Other published estimates of litter size range from 8.2 to 12.1 (Fuller et al. 1992; van Heerden et al. 1995; Maddock 1999), however, so we used a conservative range of 8.0–11.0. We assumed that litter size was normally distributed around the mean and standard deviations (Table 2). Variability in reproduction and survival was treated as independent, but catastrophes reduced both litter size and adult survival by the same percentage for 1 year. Females and males had the same survival rates, and carrying capacity was a constant value for each simulation. VORTEX 8.03 uses mortality rather than survival estimates, so values in Table 2 were transformed into mortality rates. Finally, we started each simulation with a stable age distribution.

Sensitivity Analysis of the Stochastic PVA Model Based on Logistic Regression

Using the stochastic PVA model described above and run in VORTEX, we created 1000 parameter sets by choosing input values from uniform distributions in the parameter ranges (Table 2). We used uniform distributions to emphasize the effects of variability in vital rates on model sensitivity and because data were insufficient to characterize distributions of vital rates. Following the approach of McCarthy et al. (1995), we conducted 10 iter-

Table 2. Range of parameter estimates used in the deterministic and stochastic models.

| Parameter | Estimate | | | SD of the estimate | | |
|---|----------|----------|---------|--------------------|----------|---------|
| | minimum | midpoint | maximum | minimum | midpoint | maximum |
| Pup survival ^a | 0.24 | 0.55 | 0.83 | 0.34 | 0.41 | 0.48 |
| Yearling survival ^a | 0.73 | 0.80 | 0.89 | 0.08 | 0.13 | 0.17 |
| Adult survival ^a | 0.73 | 0.80 | 0.89 | 0.08 | 0.13 | 0.17 |
| Litter size ^b | 8.0 | 9.5 | 11.0 | 2.5 | 3.8 | 5.0 |
| Females breeding (%) | 35 | 48 | 60 | 14 | 20 | 25 |
| Probability of catastrophe ^c | 0.01 | — | 0.16 | — | — | — |
| Severity of catastrophe ^{c,d} | 0.10 | — | 0.75 | — | — | — |
| Carrying capacity ^c | 40 | — | 500 | — | — | — |
| Initial population size | 10 | — | 100 | — | — | — |
| Abruptness parameter β | 1 | — | 50 | — | — | — |

^aEstimates based on Burrows et al. (1994).

^bLitter size divided by two for the females-only matrix model.

^cEstimates based on Ginsberg et al. (1995b).

^dA catastrophe severity of 0.1 reduced both litter size and adult survival by 90% for 1 year of the simulation.

ations of VORTEX for each parameter set to yield a data set of 10,000 observations of ending population size classified as extinct or persistent at year 50 and 100.

Logistic regression predicts a binary outcome—extinction or persistence—from continuous or categorical independent variables (Tabachnick & Fidell 1996). Logistic regression explores the relationship between the probability of occurrence of the binary dependent variable and a set of independent variables based on the logit transformation of a generalized linear model of the form

$$\text{logit}(p) = \ln\left(\frac{p}{1-p}\right) = \alpha_0 + \alpha_1 x_1 + \dots + \alpha_n x_n,$$

where p is the probability of the event occurring (e.g., extinction), x_n are the predictor variables (e.g., offspring survival or probability of disease outbreak), and α_n are the regression coefficients (Tabachnick & Fidell 1996). Direct comparison of the regression coefficients as a measure of relative impact is not generally useful because they depend on the units used to measure the independent variables (Selvin 1995). Instead, the importance of predictor variables is indicated by their standardized regression coefficients (α_n/SE_n), which is the regression coefficient divided by its standard error (SE_n). The standardized regression coefficient is a unitless quantity expressing the unique contribution of that independent variable and is scaled by an estimate of parameter variability or uncertainty (McCarthy et al. 1995; Selvin 1995; Tabachnick & Fidell 1996). If sampling error was calculated and removed from estimates of variances for vital rates, the uncertainty would be composed solely of process error (White et al. 2002). We retained the published but uncorrected variance estimates in our analysis, however, because our objective was to recreate past models to explore their sensitivity.

Logistic regression analyses of VORTEX simulation results were conducted with S-PLUS 4.0 (MathSoft 1998),

and we compared the standardized coefficients to rank each variable's importance. Logistic regression assumes that changes in parameters cause a linear change in the logit transformation of the dependent variable (McCarthy et al. 1995; Tabachnick & Fidell 1996). We checked this assumption by plotting the independent variables against the logit of the probability of extinction. Visual inspection of the plots did not reveal nonlinearity.

Other Sensitivity Analyses of the Stochastic PVA Model

We compared the results of logistic regression analyses with two other methods of sensitivity analysis for stochastic models. The first method employed the conventional approach. We first ran VORTEX 1000 times using the parameter values in Table 2 to establish a baseline value for the rate of extinction. We then repeated this process but decreased the mean value of a parameter by 10% before rerunning the model 1000 times. We did one parameter at a time, resetting each parameter to its original value before changing the next one and running VORTEX again. For survival parameters, we calculated a 10% decline and then determined the complement to yield the mortality rates required by VORTEX. The second sensitivity method explored the effects of changing each input variable in proportion to its variability. This method followed the same procedure we employed with the conventional sensitivity analysis, except that the average of each parameter value was decreased by 10% of its range. We call this approach the relative method of sensitivity analysis because the amount of parameter variability is scaled relative to the range of values it may assume. For both analyses, we used the parameter values in Table 2 and the perturbed mean value to calculate the percent change in the rate of extinction (ΔE) between the baseline simulations.

Construction and Analysis of Deterministic Matrix Models

To explore the population trends and dynamics underlying the preceding stochastic PVA model, we created Leslie-Lefkovich matrices (Caswell 2000a) with the same stage structure as in the stochastic PVA model run in VORTEX. Our goal was to determine whether the ranking of parameters by logistic regression would agree with analytical approaches used for sensitivity analysis of deterministic models. The model (Fig. 1) was based on a postbreeding survey and a 1-year time step. The probability of a pup surviving after emerging from the den until the following breeding season was S_p . The yearling stage (y) lasted 1 year, and the proportion of individuals surviving to become adults was S_y . The annual survival probability of an adult was S_a . Reproduction (F) was a composite of several demographic rates calculated separately for yearlings (F_y) and adults (F_a). Yearling reproduction was the product of litter size, yearling survival, and the probability of breeding. Likewise, F_a was the product of litter size, adult survival, and the probability of breeding. Litter size was the number of pups emerging from the den. Because we were interested in how variability in parameter values affected sensitivity analyses, we created three matrices representing good, average, and poor conditions or years based on the maximum, midpoint, and minimum of published parameter values, respectively (Table 2).

We analyzed the deterministic model with elasticities and life-stage simulation analysis (LSA). For each demographic parameter residing in the i th row and j th col-

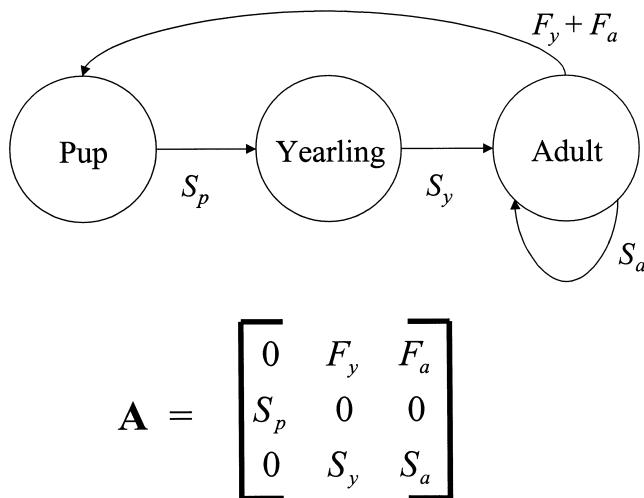


Figure 1. Life-cycle diagram and matrix model (A) used in the deterministic analyses of wild dog population dynamics. See methods for details of structure and parameterization (F_y , yearling reproduction; F_a , adult reproduction; S_p , probability of a pup surviving after emerging from the den until the following breeding season; S_y , proportion of individuals surviving to become adults; S_a , annual survival probability of an adult).

umn of the matrix, lower-level elasticity (e_{ij}) analyses were calculated according to the equations presented by Caswell (2000a) and McDonald and Caswell (1993):

$$e_{ij} = \frac{x \partial \lambda}{\lambda \partial x} = \frac{x}{\lambda} \sum_{i,j} \frac{\partial a_{ij}}{\partial x} \frac{\partial \lambda}{\partial a_{ij}},$$

where x is the demographic variable of interest, λ is the dominant eigenvalue of the matrix, and $\partial a_{ij} / \partial x$ is the partial derivative of the matrix element a_{ij} with respect to x . Lower-level elasticities decompose matrix elements into their constituent vital rates and account for vital rates occurring in multiple elements of the matrix. For the LSA of the wild dog model, we created 500 different matrices to sample a range of possible parameter space. Each matrix represented a random combination of vital rates chosen independently from uniform distributions within specific bounds (Table 2). We calculated λ for each matrix and used linear regression to assess the relationship between each vital rate and λ .

Results

Logistic regression analysis indicated that pup survival accounted for the most variability in the probability of extinction, regardless of whether or not the stochastic PVA model incorporated density dependence (Table 3). In density-dependent simulations, pup survival had over twice the effect of the next most important variable, whereas it had a 50% greater effect in density-independent simulations. Adult survival and the standard deviation of pup survival were the next most important parameters in density-dependent simulations, and the severity and probability of catastrophe were nearly as important. In the absence of density dependence, the severity and probability of catastrophes increased to the second and third most important parameters, whereas adult survival and the standard deviation of pup survival became relatively unimportant (Table 3). Although the inclusion of density dependence reduced the probability of extinction at year 100 from 0.51 to 0.33, β , which regulated the abruptness of density dependence, was the least important model parameter (Table 3). In addition, when we combined density-independent and -dependent simulations into a single logistic regression analysis, density dependence was not very important as a binary variable compared with pup survival and other parameters (columns 5 and 6 of Table 3). There were few differences in the relative importance of parameters between 50- and 100-year model projections for either density-dependent or density-independent simulations.

In contrast to the logistic regression results (Table 3), conventional sensitivity analysis indicated that adult survival caused the greatest change in extinction rate when each parameter was altered by 10% (Table 4). The standard deviation of pup survival and pup survival itself were the next most important variables. All other parameters were of negligible importance, and there were

Table 3. Standardized coefficients from the logistic regressions of the stochastic PVA model for wild dogs run in VORTEX.^a

| Variable | Density dependent | | Density independent | | Combined | |
|------------------------------|---------------------|---------------------|---------------------|---------------------|---------------------|---------------------|
| | year 50 | year 100 | year 50 | year 100 | year 50 | year 100 |
| Reproduction | | | | | | |
| density dependence | — | — | — | — | -3.61 | -4.24 |
| females breeding (%) | — | — | -9.89 | -8.95 | — | — |
| SD of females breeding | 4.39 | 2.69 | 2.46 | 4.28 | 4.29 | 4.65 |
| abruptness parameter β | 0.32 | 0.66 | — | — | — | — |
| litter size | -2.45 | -2.04 | -5.70 | -5.56 | -5.32 | -5.09 |
| SD of litter size | 0.61 | 1.10 | 1.36 | 2.57 | 0.58 | 1.61 |
| Survival | | | | | | |
| pup survival | -28.70 ^b | -33.93 ^b | -31.35 ^b | -33.34 ^b | -43.21 ^b | -47.59 ^b |
| SD of pup survival | 13.51 ^b | 16.05 ^b | 7.42 | 9.10 | 14.60 | 17.69 |
| yearling survival | -2.60 | -3.99 | -2.11 | -1.29 | -3.69 | -4.19 |
| SD of yearling survival | 1.87 | 4.34 | 3.90 | 1.85 | 3.61 | 4.44 |
| adult survival | -12.81 ^b | -15.43 ^b | -9.41 | -9.96 | -15.12 | -17.59 |
| SD of adult survival | 6.69 | 9.91 | 2.44 | 2.72 | 6.25 | 9.07 |
| Extrinsic factors | | | | | | |
| severity of catastrophe | 11.66 | 15.07 | 21.27 ^b | 23.99 ^b | 24.00 ^b | 28.18 ^b |
| probability of catastrophe | 11.09 | 13.06 | 16.64 ^b | 17.09 ^b | 19.45 ^b | 21.09 ^b |
| carrying capacity | -8.73 | -11.78 | -8.06 | -11.56 | -12.17 | -17.21 |
| initial population | -7.39 | -5.58 | -7.70 | -5.10 | -10.26 | -7.62 |
| Overall extinction rate (%) | 22.90 | 33.30 | 37.20 | 50.60 | 30.00 | 41.90 |

^aThe density-dependent and -independent simulations used 500 parameter sets and 10 iterations per parameter set. These simulations were then combined to assess the importance of density dependence.

^bThe three model parameters accounting for the most variability in the probability of extinction.

few differences between density-dependent and density-independent simulations.

Results from relative sensitivity analyses (Table 4) more closely resembled results from logistic regression

(Table 3) than results of conventional sensitivity. When each parameter was decreased by 10% of its range, the standard deviation of pup survival and pup survival itself were the most important model parameters. Adult survival

Table 4. Conventional and relative sensitivity analysis^a of the stochastic wild dog PVA model run in VORTEX indicating the percent change in extinction due to a change in parameter value.

| Variable | Density dependent | | | | Density independent | | | |
|------------------------------|--------------------|--------------------|--------------------|--------------------|---------------------|--------------------|--------------------|--------------------|
| | conventional | | relative to range | | conventional | | relative to range | |
| | year 50 | year 100 | year 50 | year 100 | year 50 | year 100 | year 50 | year 100 |
| Reproduction | | | | | | | | |
| females breeding (%) | — | — | — | — | 46.9 | 26.2 | 13.3 | 3.1 |
| SD of females breeding | — | — | — | — | -8.0 | -22.7 | -6.2 | -14.4 |
| abruptness parameter β | 13.3 | 13.8 | -13.3 | -5.1 | — | — | — | — |
| litter size | 6.7 | 8.0 | 6.7 | 8.0 | 37.2 | 17.9 | 0.9 | -7.0 |
| SD of litter size | -9.3 | -5.8 | -20.0 | -7.2 | 19.5 | -0.9 | 2.7 | -8.7 |
| Survival | | | | | | | | |
| pup survival | 70.6 ^b | 71.0 ^b | 60.0 ^b | 61.6 ^b | 84.1 ^b | 61.6 ^b | 76.1 ^b | 52.8 ^b |
| SD of pup survival | -89.3 ^b | -88.4 ^b | -88.0 ^b | -89.9 ^b | -85.0 ^b | -86.9 ^b | -90.3 ^b | -91.7 ^b |
| yearling survival | 36.0 | 18.1 | 21.3 | 12.3 | 44.2 | 22.7 | -6.2 | -10.9 |
| SD of yearling survival | 0.0 | 0.0 | 1.3 | 0.7 | 1.8 | 3.1 | -7.1 | -10.0 |
| adult survival | 168.0 ^b | 161.6 ^b | 38.7 ^b | 37.7 ^b | 131.0 ^b | 88.2 ^b | 15.0 | 7.0 |
| SD of adult survival | -2.7 | -7.2 | -13.3 | -7.2 | -11.5 | -17.0 | 2.7 | -14.4 |
| Extrinsic factors | | | | | | | | |
| severity of catastrophe | -6.7 | -18.1 | -18.7 | -18.8 | -6.2 | -13.1 | -23.9 ^b | -32.3 ^b |
| probability of catastrophe | -16.0 | -5.8 | 6.7 | -5.8 | 0.0 | -8.3 | -17.7 | -23.1 |
| carrying capacity | 17.3 | 21.7 | 13.3 | 20.3 | 12.4 | 3.1 | 9.7 | -0.9 |
| initial population size | 8.0 | 7.2 | 14.7 | 9.4 | 25.7 | 4.8 | 7.1 | -11.4 |
| Average extinction rate (%) | 7.4 | 14.1 | 7.4 | 14.1 | 11.8 | 20.9 | 11.8 | 20.9 |

^aConventional sensitivity analysis decreased each parameter by 10% of its mean value, whereas relative sensitivity analysis changed each parameter by 10% of the range.

^bThe three model parameters accounting for the most change in extinction rate.

retained some influence on the outcome of density-dependent simulations but had little effect on the probability of extinction in the absence of density dependence. Probability and severity of catastrophe became important during density-independent simulations (Table 4).

Life-stage simulation analysis of the matrix model corroborated the results of logistic regression analysis (Fig. 2). Pup survival had the strongest correlation with λ , and the percentage of females breeding was of secondary importance. Adult survival, litter size, and yearling survival accounted for little of the variation in λ . All parameters appeared to have a linear relationship with λ .

The results of lower-level elasticity analysis were more similar to those of the conventional sensitivity analysis of the stochastic model than to the logistic regression results. Elasticities of the average matrix model indicated that a small change in adult survival would have a greater instantaneous effect on population growth than would a change in pup survival (Fig. 3). But elasticities were greatly influenced by the parameter values used in the matrix. Adult survival decreased in importance, whereas all other vital rates increased in importance from bad to good years. Although adult survival had the largest elasticity in bad years, it had the smallest elasticity in good years.

Discussion

Use of Logistic Regression in Sensitivity Analysis of Stochastic PVA Models

Logistic regression allowed us to assess the relative influence of each model parameter within the range of possi-

ble values and the effect of model structure (density-dependent vs. density-independent simulations). The ability to assess multiple parameters, interactions, and variability is important when dealing with complicated PVA models, which are more realistic and whose use has accelerated in recent years (Dunning et al. 1995; Liu et al. 1995; Akçakaya & Atwood 1997). The process and theory behind the use of logistic regression for sensitivity analysis of stochastic PVA models are similar to those of the life-stage simulation analysis used on deterministic matrix models because they (1) create random sets of parameter values, (2) use those parameter sets to initialize the computer simulations, and (3) regress the results of the computer simulations against initial parameter values. Life-stage simulation analyses are used to examine variation in parameters of deterministic matrix models (Wisdom & Mills 1997), whereas logistic regression is appropriate for stochastic models in which the output of interest is extinction or persistence. Conventional sensitivity analysis of stochastic population models, which alters model parameters by a set percentage and assesses the effect on the probability of extinction (Armbruster & Lande 1993; Beissinger 1995; Woodroffe & Ginsberg 1998), seems a weaker approach to evaluating the effects of parameter variability and model structure on model results.

One of the strengths of logistic regression as a form of sensitivity analysis is the ability to assess the importance of interactions among model parameters. Interactions do not need to be incorporated explicitly into logistic regression analysis when all variables are continuous, as in this study, because the standardized coefficient indicates the relative influence of an independent variable

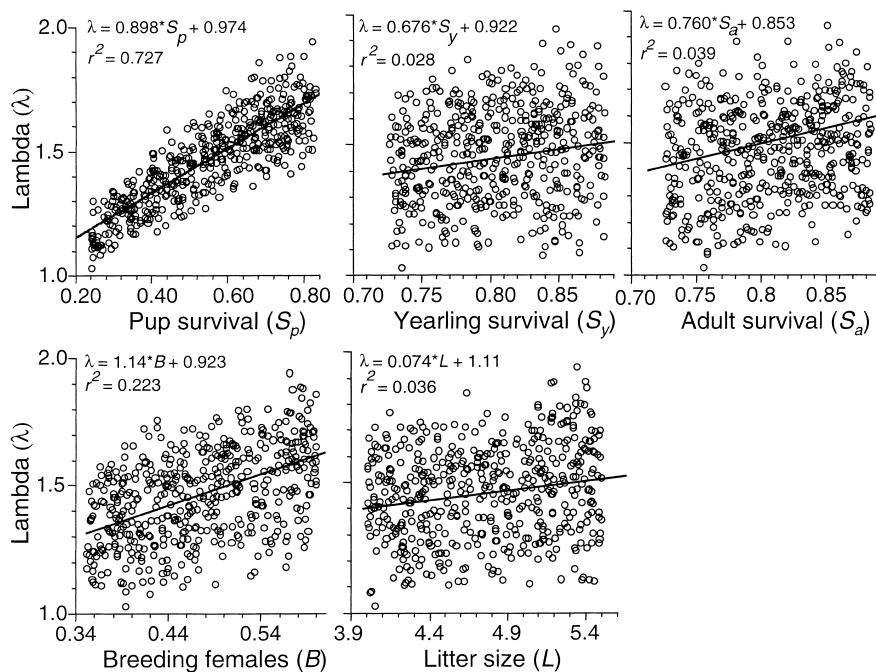


Figure 2. Life-stage simulation analysis of 500 matrices, which sampled the range of parameter values (Table 2), and the resulting population growth rate, λ . The linear regressions predict λ based on each of the five parameters in the deterministic matrix model in Fig. 1.

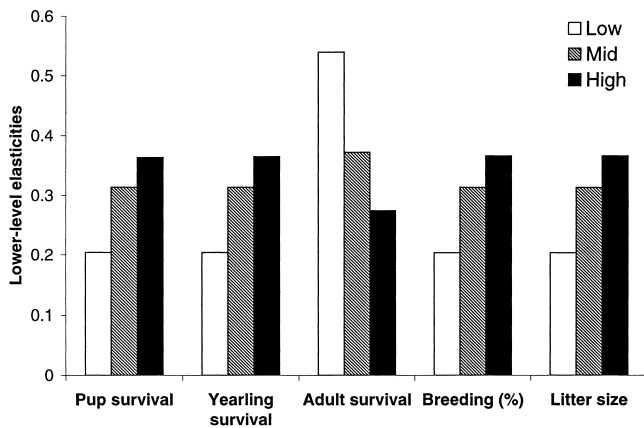


Figure 3. Lower-level elasticities calculated from the population matrices when parameters were at their minimum, midpoint, and maximum values, representing poor, average, and good years, respectively (Table 2).

while allowing all other continuous variables to vary at random. If the number of categorical parameters is small, then all possible interactions can be assessed, leading to a better understanding of population dynamics (McCarthy et al. 1995). But as the number of categorical model parameters increases, the number of possible interactions increases exponentially, requiring thousands of simulations for robust results. In addition, three-way or more complex interactions become difficult to conceptualize. In cases where many parameters are categorical, the investigator will have to choose a priori which interactions may be important to test in the logistic regression. Drechsler (1998) presented a complicated method to determine those parameter combinations that encompass most of the variability in the output of the model.

There are several weaknesses inherent in the use of logistic regression to evaluate the sensitivity of PVA models. One drawback is that the standardized coefficients are not comparable between studies. The coefficients are a function of the number of simulations and the probability associated with the outcome variable. More simulations will be necessary to solidify the ranking hierarchy of parameters for models with a large number of parameters or when only a small number of populations persist, which makes it difficult for maximum-likelihood estimators to calculate the regression coefficients. Therefore, it may often be the case that only the relative importance of variables can be compared between different analyses and studies. A second weakness is the dependence of logistic regression on accurate estimates for the range of values that model parameters may undergo. Accurate estimates of the range or variance of a vital rate requires many years of study (Beissinger & Westphal 1998) and more data than are needed to accurately estimate average rates. Uncertainty in the results of logistic regression analysis is likely to be proportional to the

number of years of field study used to estimate the range of vital rates. For studies of less than a decade, uncertainty in results due to changes in parameter ranges should be explored fully.

In summary, logistic regression is a powerful complement to other methods of sensitivity analysis, especially when parameter interactions and nonlinearities are likely to be important. The results may not be comparable between studies, however, and comparing numerous categorical variables with continuous variables may be difficult.

Comparison of Sensitivity Methods

We found some encouraging similarities among various methods of sensitivity analysis and some differences that may be explained by the range of values used in each analysis. Logistic regression, relative sensitivity analysis (i.e., altering each parameter by 10% of its range), and life-stage simulation analysis all indicate that pup survival is more important than adult survival, whereas litter size and yearling survival are relatively unimportant in explaining variation in either extinction rate or population growth. In contrast, adult survival is the most important parameter in conventional sensitivity analysis of the stochastic PVA model, which changes each parameter by 10% of its value, and in elasticity analysis of the average matrix of the deterministic model. Conventional and relative sensitivity analyses of the stochastic PVA model yield radically different estimates of the importance of adult survival and, to a lesser extent, differences in the importance of catastrophe (Table 4).

We believe that the contrasting conclusions of different forms of sensitivity analyses stem from differences in how the methods incorporate past parameter variability and in the degree of variability of model parameters (Tables 1 & 2). Pup survival varied the most, ranging from 0.24 to 0.83, whereas adult survival ranged only from 0.73 to 0.89. Methods of sensitivity analysis that account for parameter variability—logistic regression, relative sensitivity analysis, and LSA—indicate that pup survival is more important than adult survival or any other model parameter, and that catastrophe is a potentially important factor under density-independent population growth. Vucetich and Creel (1999) and Woodroffe et al. (1997) note that changes in pup survival had little effect on persistence when survival ranged from 30%–50%, but extinction rates were greatly affected when pup survival ranged more widely. Variation in demographic rates also affected the results of the elasticity analyses: adult survival had the largest elasticity during good years but the smallest elasticity during bad years (Fig. 3). Recent studies demonstrate that elasticity rankings may change with different parameter estimates (Wisdom & Mills 1997; Citta & Mills 1999; Mills et al. 1999; de Kroon et al. 2000).

In general, the results of logistic regression, relative sensitivity, and life-stage simulation analyses were more

similar to one another than to the results of conventional sensitivity and elasticity analyses. This probably occurred because the former group of methods explicitly incorporate parameter variability and are therefore primarily retrospective, whereas the latter do not and are therefore prospective (*sensu* Caswell 2000*b*). Below we discuss further implications of these differences.

Use of Sensitivity Analyses in PVA for Making Conservation Decisions

Deciding among management options may be difficult if the results of sensitivity analyses change with parameter values and method of analysis. Employing several kinds of sensitivity analyses can lead to a better understanding of model outcomes if one thinks carefully about what the analyses are examining (Table 1). Logistic regression, relative sensitivity analysis, and LSA, as they were used in this study, indicate which parameters account for the greatest amount of variability in the outcome variable. Elasticity and conventional sensitivity analysis indicate which model parameters cause the greatest effect on the outcome variable with a minute change in that parameter's average value. The multiple sensitivity analyses we used suggest that although adult survival has the greatest instantaneous effect on population growth, pup survival explains more about the variability in population growth or extinction rate, partly because pup survival is so variable. This insight has short- and long-term management implications. Changes in adult survival will probably have the greatest and most immediate effect on population size, but controlling the variability of pup survival may be a better method of minimizing population fluctuations over long periods of time.

When evaluating different approaches to sensitivity analysis, Caswell (2000*a*, 2000*b*) suggests that managers focus on prospective analyses because they indicate a functional relationship between the model input and output parameters. When prospective analyses are used to evaluate management options, it is implicitly assumed that each vital rate will undergo a perturbation of a similar proportion due to management actions. We know of no reason why this should be true; to the contrary, empirical results suggest that parameters with high elasticities tend to have low natural variability (Ehrlén & van Groenendael 1998; Gaillard et al. 1998; Pfister 1998; Sæther & Bakke 2000). In long-lived birds, for example, some vital rates can be greatly increased (e.g., nesting success through double clutching and nest site protection), whereas others can be elevated only slightly even though they have a higher elasticity (e.g., adult survival through predator control; Hiraldo et al. 1996).

The effects of a management action on population dynamics result from the combination of how much a vital rate can be perturbed and its relative effect on popula-

tion growth (i.e., elasticity) or extinction rate (i.e., sensitivity measured by logistic regression or other methods). Thus, a more accurate assessment of the potential effects of different management activities would first quantify the degree to which a management action can alter targeted model parameters (e.g., vital rates) and would then determine the potential effects of management scenarios directly by estimating a new lambda that would result from a particular management action. Strategies could be rated by a combination of the effects on recovery and cost. Until the potential effects of various management strategies are quantified, one might assume that parameters with low variability are tightly constrained and may be less affected by management actions.

By conducting several different sensitivity analyses with multiple model structures, we generated results that help interpret conflicting conclusions from previous modeling studies of wild dog population dynamics. Using the same stochastic PVA model, Burrows et al. (1994) and Ginsberg et al. (1995*b*) concluded that catastrophes, carrying capacity, and density dependence are important parameters. Although the inclusion of density dependence greatly affected our model outcomes, logistic regression analyses and conventional and relative sensitivity analyses indicate that carrying capacity and the abruptness of density dependence do not explain as much of the variation in extinction rate as did pup survival, adult survival, and the standard deviation of pup survival (Tables 3 & 4). Differing assumptions about density dependence result in contrasting conclusions about the importance of catastrophes (Burrows et al. 1994; Ginsberg et al. 1995*b*). Catastrophes have a greater effect on extinction rate in our density-independent simulations.

From our results and PVA models presented previously (Burrows et al. 1994; Ginsberg et al. 1995*b*), it is difficult to determine whether the extinction of the Serengeti wild dog population is more likely to be due to chance alone (Ginsberg et al. 1995*b*) or to invasive research methods (Burrows 1992). We do not believe that PVA can answer such a question because models rarely produce accurate estimates of the likelihood of extinction (Ludwig 1999; Fieberg & Ellner 2000). To do so, the model structure and parameter estimates would have to be both precise and accurate. A more pragmatic approach is to hope that a PVA model captures the important dynamics of a system and addresses questions of relative importance, such as which management action will be more effective, rather than generate accurate estimates of extinction probabilities (Beissinger & Westphal 1998).

Finally, we caution against the use of sensitivity analysis as the only basis for management decisions. Sensitivity analysis does not indicate which variable might be causing a population decline or limiting population growth (Green & Hiron 1991; Beissinger & Westphal 1998). For

example, lions (*Panthera leo*) and hyenas (*Hyaenidae*) have a large effect on the persistence of wild dog populations through predation and competition (Creel & Creel 1996; Carbone et al. 1997; Gorman et al. 1998). Thus, wild dog populations may be regulated by lion and hyena densities (Vucetich & Creel 1999), which were not included in our models, rather than by the most influential model parameter. Nonetheless, sensitivity analysis can be a powerful way to understand some of the underlying processes driving population dynamics and the relative importance of different input variables affecting model outcomes.

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