

**Demographic analysis of the black-footed ferret in the Conata Basin – Badlands National
Park, South Dakota**

Great Plains Cooperative Ecosystem Studies Unit

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Background

The reintroduction of the endangered black-footed ferret (*Mustela nigripes*) to Badlands National Park and adjacent areas of Conata Basin beginning in 1994 has been a key element of the species' recovery. By early in this decade, the Conata Basin – Badlands National Park population had attained the largest size of any free-ranging population. Previous population studies of the species in the wild are limited to that near Meeteetse, Wyoming by Forrest et al. (1988). They reported minimum number known alive for summers 1983-85, mark-reobservation estimates of population size with associated variances (MNKA) for 1984-85, and sex ratios and juvenile/adult ratios for various years. The Conata Basin – Badlands National Park population has been productive enough to serve as the source for translocations to several other sites. This "harvesting" of ferrets has led to questions about its effects on the source population, in part prompting the current study. Here we develop matrix models for the demography and population dynamics of the black-footed ferret in Conata Basin – Badlands National Park, South Dakota. Matrix population models generate a wide array of useful measures concerning life histories. For example, the dominant eigenvalue, λ , integrates much of the information on population dynamics and acts both as a measure of evolutionary fitness at the individual level (Caswell, 2001:295) and as a measure of growth rate of the population. Our major goal was to provide a synthetic approach that could guide management decisions when considering possible harvest of ferrets for translocations to other reintroduction sites, as well as when considering land use alternatives. We also sought to provide managers with an updated summary of the life history and population dynamics of black-footed ferrets.

Methods

We used encounter histories for 390 wild-born black-footed ferrets from three colonies in Conata Basin over six years (1999-2005). These data were the basis for a life-cycle graph (Fig. 1) and a matrix population analysis with an annual post-breeding census (Cochran and Ellner 1992, McDonald and Caswell 1993, Caswell 2001) for Conata Basin, South Dakota. The data were age-specific, so the model has four age classes. S. Breck of the National Wildlife Research Center, Fort Collins, CO used program *MARK* to estimate annual survival rates in two age

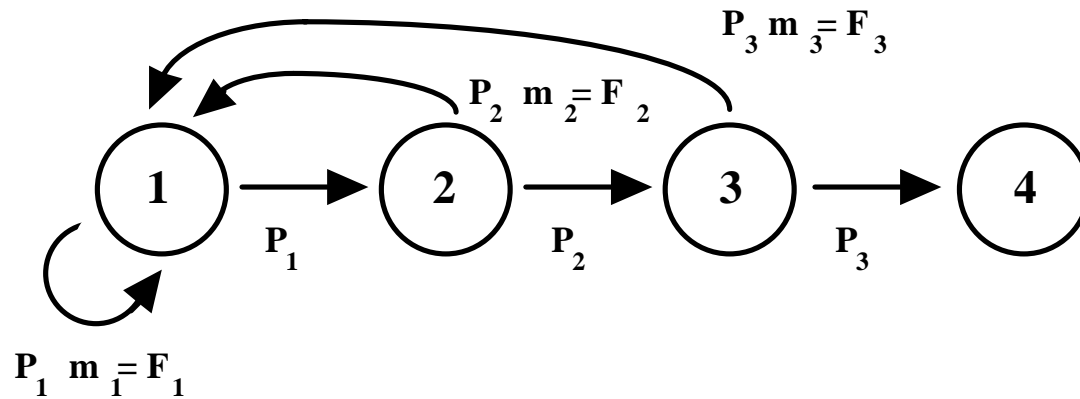


Figure 1. Generalized life cycle graph for black-footed ferret. The circles denote age-classes. The arrows depict vital rates (survival or fertility) that involve transitions between the age-classes. Note that fertility transitions (F_i) are the product of terms describing the production of offspring (m_i), and terms (P_i) describing the survival of the mothers from the time of the annual census, just after the breeding season, until they produce kits just before the next census.

classes: animals about 3 - 15 months of age, roughly corresponding to the first year of life, and adults (animals > 15 months of age). A goodness-of-fit test ($\chi^2 = 17.36$; $df = 16$) showed that the data were not overdispersed, so he proceeded with AICc as a model selection criterion. He estimated survival with the Cormack-Jolly-Seber model, which provides estimates of apparent survival rates (apparent survival is equal to true survival when emigration is 0) and capture probabilities. He ran nine models to examine the importance of age (juvenile or adult), sex (male or female), and time (the 6-year period). The top model (AIC weight = 0.47, twice the support of the nearest contender) estimated juvenile female survival as 0.698, adult female survival as 0.498, and lumped juvenile and adult male survival as 0.375. The data did not support differences in apparent survival across years. Because the matrix model assumed female demographic dominance, we use only the female survival rates hereafter.

The timing of the survey, relative to the time of litter size estimation, posed a challenge to estimating the vital rates. The annual survey occurred between late August and October, three months after the time at which litter sizes were estimated. For most vertebrates survival is lowest in the first year and rises to a peak near the age of first reproduction. We therefore adjusted monthly survival (4th through 15th month) to rise (using a logistic growth function) from an annualized rate of 0.27 in the first month to an annualized rate of 0.81 in the 15th month, subject to the constraint that the overall survival over the one-year period must equal the estimate

of 0.698 under the *MARK* analysis. We then back-calculated survival during the first three months using the same algorithm, arriving at an adjusted first-year (first to 12th month) survival rate of 0.57. Second and third-year survival followed the original *MARK* estimate of 0.498.

The model has two kinds of input terms, P_i describing survival rates, and m_i describing number of female offspring per female (Table 1). Fertility terms, F_i , occur in the top row of the matrix and represent the product of an m_i term and a P_i term that tracks the mother's survival from the time of the post-breeding survey until the time she actually breeds almost one year later (assuming a survey interval of one year). We calculated an array of matrix measures using *Mathematica*TM programs written by D.B. McDonald, largely using algorithms found in Caswell (2001).

Table 1. Mean \pm SD vital rates of black-footed ferrets in Conata Basin, South Dakota, 1999-2005, derived from matrix population modeling.

Vital rate	Value
m_1	1.49 \pm 0.28
m_2	1.68 \pm 0.42
m_3	1.75 \pm 0.29
P_1	0.57 \pm 0.21
P_2	0.569 \pm 0.19
P_3	0.498 \pm 0.19

A useful indication of the state of the population comes from the sensitivity and elasticity analyses. Sensitivity is the effect on population growth rate (λ) of an absolute change in the vital rates (a_{ij} , the arcs in the life cycle graph [Fig. 1] and the cells in the matrix, \mathbf{A} [Fig. 2a, b]). Sensitivity analysis provides several kinds of useful information (Caswell 2001). First, sensitivities show "how important" a given vital rate is to population growth rate (λ) or fitness. For example, one can use sensitivities to assess the relative importance of survival (P_i) and reproductive (F_i) transitions. Second, sensitivities can be used to evaluate the effects of inaccurate estimation of vital rates from field studies. Inaccuracy will usually be due to paucity

of data, but could also result from use of inappropriate estimation techniques or other errors of analysis. In order to improve the accuracy of the models, researchers should concentrate additional effort on transitions with large sensitivities. Third, sensitivities can quantify the effects of environmental perturbations, wherever those can be linked to effects on stage-specific survival or fertility rates. Fourth, managers can concentrate on the most important transitions. For example, they can assess which stages or vital rates are most critical to increasing the population growth (λ) of endangered species or the "weak links" in the life cycle of a pest. Fifth, the sensitivities are directly equivalent to selection gradients in quantitative genetics. They therefore represent the direct force of selection acting on a trait. In this case, the traits are the vital rates (survival and fertility) that largely determine the population dynamics. Any heritable variation in vital rates to which λ is highly sensitive should therefore be expected to respond to natural selection.

Elasticities are useful in addressing situations in which changes in the vital rates are proportional rather than additive. Elasticities are the sensitivities of λ to proportional changes in the vital rates (a_{ij}) and have the useful property of summing to 1.0. The difference between sensitivity and elasticity conclusions results from the weighting of the elasticities by the value of the original arc coefficients (the a_{ij} cells of the projection matrix). Management conclusions will depend on whether changes in vital rates are likely to be absolute (guided by sensitivities) or proportional (guided by elasticities). By using elasticities, one can further assess key life history transitions and stages as well as the relative importance of reproduction (F_i) and survival (P_i) for a given species.

Stochastic matrix projections allow the vital rates to vary, providing a realistic addition to demographic modeling. For the variances of the vital rates used in the stochastic matrix projections, Breck used a random effects model to separate process from sampling variance. Preliminary stochastic matrix projections using the original variance estimates showed drastic effects on λ (e.g., reduction from $\lambda = 1.34$ to $\lambda = 0.93$). We therefore used a moderated variance estimate, whereby we chose the standard deviation of the vital rates from the larger of the following: either the original estimate, or 3/16 of the corresponding vital rate. On each iteration of the matrix projection, the vital rates were selected from a beta distribution (Morris and Doak 2002, p. 275), with means and standard deviations (Table 1) as determined above. The vital rates selected at each iteration were uncorrelated, since the data were insufficient to produce reliable estimates of potential positive or negative correlations between the set of vital rates. Each run

consisted of 1,000 survey intervals (years) beginning with a population size of 1000 distributed according to the Stable Age Distribution (SAD) under the deterministic model. Beginning at the SAD helps avoid reaching conclusions based on the effects of transient, non-equilibrium dynamics. The overall simulation consisted of 100 runs (each with 1,000 cycles). We calculated the stochastic growth rate, $\log \lambda_s$, according to Eqn. 14.61 of Caswell (2001).

Results

Fig. 2a shows the symbolic terms in the demographic projection matrix corresponding to the life cycle graph of Fig. 1. Fig. 2b gives the corresponding numeric values.

F_1	F_1	F_1	–
P_1	–	–	–
–	P_2	–	–
–	–	P_3	–

Figure 2a. Symbolic projection matrix corresponding to the life cycle graph of Fig. 1 for the matrix demographic analysis of black-footed ferrets in Conata Basin, South Dakota, 1999-2005. Fertility transitions are in the top row. Survival transitions are along the subdiagonal.

0.848	0.838	0.872	–
0.57	–	–	–
–	0.498	–	–
–	–	0.498	–

Figure 2b. Numerical values for the projection matrix for females.

The model yielded a deterministic λ (population growth rate) of 1.34, indicating a 34% per-year rate of population growth. As shown below, environmental stochasticity acts to dampen this strong estimated rate of increase. Adjusting first-year survival downward serves as a way of

simulating “harvest” of first-year animals for translocation to other reintroduction sites. Harvest of as many as 32% of the first-year animals would reduce λ to 1.04, above the level (1.0) required to maintain a growing population.

Fig. 3a shows the “possible sensitivities only” matrix. Fig. 3b shows the matrix in the form of the percentage of the total sensitivity in each of the cells (unlike the elasticity, the sensitivities do not sum to 1.0).

0.68	0.289	0.107	–
0.589	–	–	–
–	0.188	–	–
–	–	0	–

Figure 3a. Untransformed sensitivities of λ to changes in the vital rates. The three transitions to which λ is most sensitive are in bold font. Only values that correspond to non-zero cells in the original matrix (Fig. 2) are shown.

36.7	15.6	5.8	–
31.8	–	–	–
–	10.2	–	–
–	–	0	–

Figure 3b. Sensitivities of λ to changes in the vital rates, shown as percentages of the total, for black-footed ferrets in Conata Basin, South Dakota, 1999-2005. The three transitions to which λ is most sensitive are in bold font.

In general, changes that affect one type of age class or stage will also affect all similar age classes or stages. For example, any factor that changes the annual survival rate of second-year females is likely to cause similar changes in the survival rates of third-year females. It is, therefore, usually appropriate to assess the summed sensitivities for similar sets of transitions (vital rates). The summed sensitivity of λ to changes in fertility has the greatest importance (58.1% of the total sensitivity). Furthermore, arcs emerging from the first node (P_1 and F_1) account for 68.6% of the total sensitivity. The major conclusion from the sensitivity analysis is that first-year and fertility transitions have the greatest impact on population growth.

Elasticities for the ferret model are shown in Fig. 4. λ is most elastic to changes in first-year fertility (F_{11} , the self-loop on the first node in Fig. 1) followed by first-year survival (P_{21}) and second-year reproduction (F_{21}). The sensitivities and elasticities correspond in rank magnitude, but the relative importance of first-year fertility is greater for the elasticities. The summed reproductive elasticities accounted for 68% of the total elasticity. Thus, fertility, and to a lesser extent first-year survival, are the data elements that warrant careful monitoring in order to refine the matrix demographic analysis. Because of the high variability in the estimates of the vital rates, further data would be useful in more accurately determining whether the variability is an inherent feature of the natural history (process variance) or an artifact of small sample size (sampling variance).

0.43	0.18	0.07	–
0.25	–	–	–
–	0.07	–	–
–	–	0	–

Figure 4. Elasticities of λ to changes in the vital rates for black-footed ferrets in Conata Basin, South Dakota, 1999-2005. The three transitions to which λ is most elastic are in bold font. Elasticities always sum to 1.

van Groenendaal et al. (1994, as refined by Wardle 1998) developed a method of decomposing a life history into distinct loops based on elasticities. The ferret model has three distinct reproductive loops, one from each of the first three nodes. The values for the three loops are given in Table 2. The major conclusion is that the most important loop emanates from first-year individuals (43.8% of the total loop elasticity).

Table 2. Loop analysis for matrix analysis for black-footed ferrets in Conata Basin, South Dakota, 1999-2005.

Description	Value (%)
Loop from Age-class 1	43
Loop from Age-class 2	36
Loop from Age-class 3	21

Lower level elasticity analysis (Caswell 2001, p. 232) allows one to decompose the elasticities to assess the contributions of the component terms. The elasticity results provided above are for the entire arcs/transitions in the life cycle graph. In this case, the fertility transitions, $F_i = P_i * m_i$, are the products of two kinds of terms -- m_i , describing offspring per female, and P_i , describing the survival rate of the female parents. We can decompose the elasticities into the contribution of each of these two kinds of terms. The summed lower level elasticities for survival terms (P_i) accounted for 59.5% of the total lower level elasticity, vs. 40.5% of the total accounted for by offspring production terms (m_i). Half of the elasticity value of each of the fertility (F_i) terms stems from its P_i component and half from its m_i component. This result somewhat tempers the earlier conclusion of the paramount importance of fertility. It becomes clear, here, that the contribution of the survival of the mothers (the P_i component of the F_i term) is critical. Because of their contributions to the fertility arcs, and their stand-alone importance in the survival transitions (P_i), the survival rates are of considerable importance. The critical importance of the first year of life to the population dynamics of black-footed ferrets is illustrated by the importance of the first-year lower level parameters. Together, first-year offspring production (m_1) and first-year survival (P_1) account for 66.1% of the total elasticity of λ to changes in lower level terms.

The stable age distribution (SAD, Table 3) describes the proportion of each age-class or stage in a population at demographic equilibrium. Under a deterministic model, any unchanging matrix will converge on a population structure that follows the stable age distribution, regardless of whether the population is declining, stationary or increasing. Under most conditions, populations not at equilibrium will converge to the SAD within 20 to 100 census intervals. For ferrets at the time of the annual post-breeding census (just after the end of the breeding season), new offspring represent 61 % of the population, while yearling first-time breeders represent 26%

of the population. At the time of the annual census, fewer than 4% of the population will be fourth-year females that have just bred for the last time.

Table 3. Modeled stable age distribution for black-footed ferret in Conata Basin, South Dakota, 1999-2005.

Age-class	Wild-born
1	0.609
2	0.259
3	0.096
4	0.036

Reproductive values (Table 4) can be thought of as describing the “value” of a stage as a seed for population growth relative to that of the first (newborn) stage (Caswell 2001). The reproductive value is calculated as a weighted sum of the present and future reproductive output of a stage discounted by the probability of surviving (Williams 1966). The reproductive value of the first stage is always 1.0. For example, a second-year female (Age-class 2) is “worth” 0.865 offspring. The cohort generation time for ferrets was 1.67 years (SD = 0.8 years). Again, this emphasizes the importance of relatively rapid turnover in ferret populations in Conata Basin, with a strong importance of first-year survival and reproduction.

Table 4. Modeled reproductive values for the lack-footed ferret in Conata Basin, South Dakota, 1999-2005.

Age-class	Reproductive value
1	1
2	0.87
3	0.65
4	0

The stochastic model (Table 5) produced two major results. First, variance in the vital rates had a major dampening effect on our estimate of λ (reducing it from 1.34 to 0.995). Second, it

showed that vulnerability is highest in the initial stages of population growth. Of 100 simulated populations, six went pseudoextinct (<5 individuals remaining), all within the first 50 census intervals. The remaining populations all grew to very large size, because the simulation put no upper bound on the maximal population size. The magnitude of stochastic fluctuation, driven by the estimated standard deviations of the vital rates, largely determines the negative impact on population dynamics. This negative effect occurs despite the fact that the average (expected) vital rates remain the same as under the deterministic model. This apparent paradox is due to the log-normal distribution of stochastic ending population sizes (Caswell 2001). The log-normal distribution has the property that the mean exceeds the median, which exceeds the mode. Any particular realization will therefore be most likely to end at a population size considerably lower than the initial population size. These results indicate that populations of ferrets may be vulnerable to high levels of stochastic fluctuations in their vital rates.

Table 4. Summary of stochastic projections of the black-footed ferret matrix population model.

Note that the stochastic λ (0.995) is considerably lower than the deterministic λ (1.34).

	Factor or value
Input factors:	
Affected cells	All
SD of random beta distribution	Empirical or 3/16 of mean (cf. Table 1)
Output values:	
Deterministic λ	1.34
# Extinctions / 100 trials	6
# Declines / # survived pop	0/94
Log λ_s	-0.005
λ_s	0.995
% reduction in λ	25.8

Variation in the vital rates can profoundly influence the life history of the black-footed ferret, and therefore affect management options. Pfister (1998) showed that for a wide range of

empirical life histories, high sensitivity or elasticity was negatively correlated with high rates of temporal variation. That is, most species appear to have responded to strong selection by having low variability for sensitive transitions in their life cycles. A possible concern is that anthropogenic impacts may induce variation in previously relatively invariant vital rates (such as "adult" survival), with consequent detrimental effects on population dynamics. For black-footed ferrets, because stochasticity acting on early vital rates will have particularly strong negative impacts, the opportunities for adjustment of risk load may be limited compared to the opportunities in species with different life histories. The highly variable vital rates estimated here may predispose ferrets to relatively high risk of local extinction balanced by a reasonably high likelihood of profiting from opportunities provided by favorable changes in habitat or prey base. Establishment of replicated and connected populations and, where possible, buffering against variation in early vital rates may be key to long-term persistence of ferrets in the wild.

Discussion

Clearly, the better the data on vital rates and the nature and source of variance in those vital rates, the more reliable the resulting analytical results will be. Additional data from this and other populations on the range of variability in the vital rates would allow more realistic functions to model stochastic fluctuations. For example, time series based on actual temporal or spatial variability would allow construction of a series of "stochastic" matrices that mirrored actual variation. One advantage of such a series would be the incorporation of observed correlations between fluctuations in vital rates. Using observed correlations would improve on this assumption by incorporating forces that we did not consider. Those forces may drive greater positive or negative correlation among life history traits. Other potential refinements include incorporating density-dependent effects. At present, the data appear insufficient to assess reasonable functions governing density dependence. Although the total census data suggest a flattening of the population growth, any such conclusion may be confounded by the transition from the fairly regular supplementation with captive-bred ferrets prior to 2000 vs. the virtual cessation of the practice afterward. In species with high rates of natal and breeding dispersal, mark-recapture analyses estimate only *apparent* survival. Many surviving individuals could be missed if they leave the study areas. The drawback of missing dispersers is largely tempered, in the present analysis, by our reliance on female-only data. In mammals in general, and in solitary carnivores in particular (Sandell 1989), females are more sedentary than males. More complete

understanding will require cooperation by field biologists over large areas and the use of telemetry and other tools that can establish the proportions of dispersers and the range of distances covered by dispersers as a function of age, sex, and breeding status.

Our major conclusions on the basis of the matrix model analyses are that

1. Early survival and reproduction rates are critical to ferret population dynamics. The stochastic, sensitivity, elasticity and loop analyses all point to the critical importance of these early transitional rates.
2. High levels of variability in vital rates mean that rates of population growth may vary from extremely high ($\geq 50\%$ per year) to stationary or even slightly declining. None of this incorporates the more drastic influence of extrinsic agents of mortality such as plague epizootics, which were not noted in Conata Basin during the study period.
3. Population growth rates likely will vary widely in both space and time. Local extinctions may be a regular occurrence, but opportunities for colonization or recolonization of vacant habitats likely is critical to landscape level persistence.
4. Critical data for improved understanding of population dynamics include survival rates that incorporate the probabilities of natal and breeding dispersal and documentation of the comparative effects on local vital rates in areas from which ferrets are harvested for relocation versus areas in which no harvesting takes place.
5. Harvest of first-year animals at a reasonably high level (as high as one-third of those available in early autumn) may be possible without jeopardizing the well-established Conata Basin population. Although the stochastic simulations might seem to suggest a narrow margin of safety between an increasing ($\lambda > 1$) and a declining population, it is likely that positive density dependence would reduce variation in the vital rates and boost their means when population density declined. Certainly the very high initial growth of the population suggests that the capacity for increase in uncrowded habitats is very high. Any slight risks of harm to the Conata Basin population must also be weighed against the potentially very large benefits of establishing vigorous alternative wild-breeding populations from the apparently vigorous wild-born animals

produced in Conata Basin, which likely survive better at release sites than do captive-reared animals.

Management recommendations

1. Harvest, at reasonable levels, of wild-born black-footed ferrets from Conata Basin for translocation to other reintroduction sites is unlikely to pose risks to the viability of the Conata Basin population. We recommend that the practice continue.
2. Our demographic analyses of the black-footed ferret population at Conata Basin are consistent with the species being fairly "weedy," as evidenced by the overwhelming importance to population performance and persistence of first-year survival and fertility. Managers should begin to think of the black-footed ferret as a species capable of rapid population growth in suitable resource conditions, but vulnerable to rapid population decline as well. Strategies for species recovery should take into account these attributes, possibly emphasizing loosely connected subpopulations that can be expected to increase and decrease in distribution and abundance rapidly. This is a departure from traditional thinking regarding endangered species life histories and recovery strategies.

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