

THE DYNAMICS AND VIABILITY OF THE  
ENDANGERED STREAKED HORNED LARK  
(*Eremophila alpestris strigata*)

by

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A Thesis  
Submitted in partial fulfillment  
of the requirements for the degree  
Master of Environmental Studies  
The Evergreen State College  
June 2009

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## ABSTRACT

### THE DYNAMICS AND VIABILITY OF THE ENDANGERED STREAKED HORNED LARK (*Eremophila alpestris strigata*)

Adam W. Schapaugh

The Streaked Horned Lark (*Eremophila alpestris strigata*) is an endangered songbird endemic to prairie and open coastal habitats west of the Cascade Mountains. Its persistence is handicapped by dramatic habitat loss, human disturbance and predation. Fewer than 1,000 individuals remain in four isolated subpopulations across Washington and Oregon. By combining demographic data and information on size and distribution of local populations, I developed a stage- and space-structured demographic model to analyze *E. a. strigata*'s viability in Washington State. Importantly, simulations that include variation and correlation in survival rates yield variable, yet qualitatively consistent, forecasts of population growth. The model predicted a continuing statewide population decline and near certain risk of extinction over the next 25 years. To determine where conservation efforts and data collection are best focused, I performed a series of perturbation analyses in which the effects of changing vital rates were quantified. I found that population growth is most sensitive to the survival of adults. Under a modest scenario, increasing the survivorship of adults by 10% was sufficient to lengthen the median time to extinction by more than 5 years. A more optimistic improvement (20%) yielded a viable Coastal subpopulation. In contrast, I found that some well-meaning management activities, in particular efforts solely targeting fecundity, are unlikely to be either cost effective or biologically sound. Although many anthropogenic impacts threaten *E. a. strigata*, the subspecies' future could be bright, provided that research and management focus on biologically significant aspects of its life history. However, I demonstrate that complacency is ill-advised; decisive action to quickly improve demographic rates is needed, given the consistent qualitative output across models and the inherent uncertainty in predictions of future population trends.

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## **ACKNOWLEDGMENTS**

Many thanks to Dr. Alison Styring (The Evergreen State College, MES program) for serving as my primary advisor and her two years of support, excellent review, and encouragement during my time in the MES program. I also thank Dr. Scott Pearson of the Washington Department of Fish and Wildlife for providing the data that formed the core of my thesis and for his excellent feedback, ideas, and support. I also thank Dr. Rob Knapp (The Evergreen State College, MES program) for serving as a reader and for his timely and constructive comments. Lastly, for her enduring love and encouragement, I thank my wife, Jami.



## INTRODUCTION

Globally, habitat loss and degradation has precipitated widespread declines in many grassland birds (Askins 1995, Donovan and Flather 2002). This is true of the Streaked Horned Lark (*Eremophila alpestris strigata*), a rare subspecies of Horned Lark endemic to the Pacific coast of North America (Pearson and Altman 2005). Historically, *E. a. strigata* occupied prairie and open coastal habitats west of the Cascade Mountains in British Columbia, Washington and Oregon (Stinson 2005). However, the amount of suitable habitat has contracted over the past century, due primarily to the intensification of agriculture and urban development. Not coincidentally, *E. a. strigata* has been extirpated from much of its historic range and is now confined to small pockets of isolated habitat in Washington and Oregon (Stinson 2005). The global population is likely below 1,000 individuals (Pearson and Hopey 2005); distributed among four spatially distinct subpopulations in the south Puget Sound, lower Columbia River, Washington coast, and Willamette Valley (Rogers 2000; Stinson 2005).

Despite documented shifts in the subspecies breeding range (e.g. Rogers 2000), the rapid decline of *E. a. strigata* has gone largely unnoticed. Not discounting nearly a decade of applied research by the Washington and Oregon Department's of Fish and Wildlife, long-term ecological information is limited, as have been quantitative evaluations of the subspecies status (but see Pearson et al. 2008). Here, I present a viability analysis of the three remaining subpopulations of *E. a. strigata* in Washington State. I combined demographic data and information on size and distribution of each of the subpopulations to construct a stage- and space-structured stochastic model, which I used to (1) determine the likely outcome of current population processes; (2) examine explicitly the separate influences of fecundity, adult survival, and juvenile survival on population dynamics; and (3) predict the consequences of alternative recovery actions.

My use of stage-based models for population viability analysis differs from many published population models in two ways. First, I pay particular attention to the importance of temporal variability, using straightforward estimates of survival variation from field data. Second, I use the models not only to address threats, but also to ask how best to prioritize future data collection. Although there is more demographic data on *E. a. strigata* than is often available for endangered species, significant gaps and uncertainties do compromise some of the results. Thus, I use the models to draw conclusions about the relative benefits of further research on different life stages. Ideally, this work will prove to be beneficial for the conservation of *E. a. strigata*, but also to

evaluate the applicability of theoretical concepts (e.g. nonequilibrium dynamics) applied to the management of endangered songbirds in fragmented landscapes.

### **TAXONOMY AND CONSERVATION STATUS**

The Horned Lark (*Eremophila alpestris*) is a member of the family *Alaudidae* (larks) in the order *Passeriformes* (Sibley 2000). It is a small ground-nesting passerine native to both the New and Old Worlds (Stinson 2005). Across North America, there are 21 described subspecies based primarily on differences in size and plumage color (American Ornithologists' Union 1957). *E. a. strigata* was first described by Henshaw (1884), based on specimens collected in Pierce County, Washington (Stinson 2005). Each individual is marked by a dark breast-band, lores, and malar stripe that contrast with the yellow to white supercilium. The sexes can be distinguished by the male's brighter plumage and larger body (Beason 1995). In size and appearance, *E. a. strigata* most closely resembles *E. a. insularis* of the California Channel Islands, but is characterized by a less heavily streaked breast and bright yellow on the abdomen and flanks (Behle 1942).

Today, *E. a. strigata* is a federal candidate for listing under the Endangered Species Act by the U.S. Fish and Wildlife Service. In Canada, it is recognized by the Committee on the Status of Endangered Species and is Red-listed in British Columbia. In Oregon, it is considered a state-sensitive species by the Department of Fish and Wildlife. Following the completion of a range-wide assessment and preliminary conservation strategy by Pearson and Altman (2005), the subspecies was listed as endangered by the Washington Department of Fish and Wildlife on March 2, 2006.

### **DISTRIBUTION AND HABITAT ASSOCIATIONS**

Historically, *E. a. strigata* bred in prairie and open coastal habitats from the southwestern corner of British Columbia, through the Puget Trough, and as far south as Eugene, Oregon (Fig. 1a) (Stinson 2005). Early authors describe the breeding range as including the Sierra Nevada and Channel Islands of California (Gabrielson and Jewett 1940), but Behle (1942) later assigned these groups to *E. a. insularis* and *E. a. sierra*. In Washington, *E. a. strigata* was largely confined to the glacial outwash prairies of the south Puget Sound region. However, the subspecies could be found in areas of the northern Puget Trough, along the Pacific coast extending northward from Willapa Bay, and on islands of the Columbia River (Jewett et al 1953). In Oregon, *E. a. strigata* was a common breeder throughout the Willamette and Rogue River valleys in the western half of the state (Stinson 2005). As recently as the 1940's, individuals were commonly seen

in the rangelands of Linn and Benton Counties and the grasslands east of Medford (Gabrielson and Jewett 1940).

Today, more than 90% of the original grassland habitat has been lost in the south Puget Sound (Crawford and Hall 1997). Across Washington State, distribution surveys conducted by Rogers (1999) and Maclaren and Cummins (2000) found only 11 nesting sites occupied. Subsequent survey work by Pearson and Hopey (2004, 2005) indicate a small likelihood of finding additional nesting locations, as most sites with potentially suitable habitat have already been surveyed. In Oregon, nearly all (>99%) of the pre-settlement grasslands are gone (Johannessen et al. 1971; Towle 1982), thus confining the subspecies almost entirely to the Willamette Valley (Fig 1b) (Rogers 2000). Most current sightings come from Marion and Polk Counties, especially on and around Basket Slough National Wildlife Refuge (Altman 2000). Other small, scattered groups may be found in the lightly populated areas between Peoria and Harrisburg, and southeast of Portland near Estacada (Altman 1999).

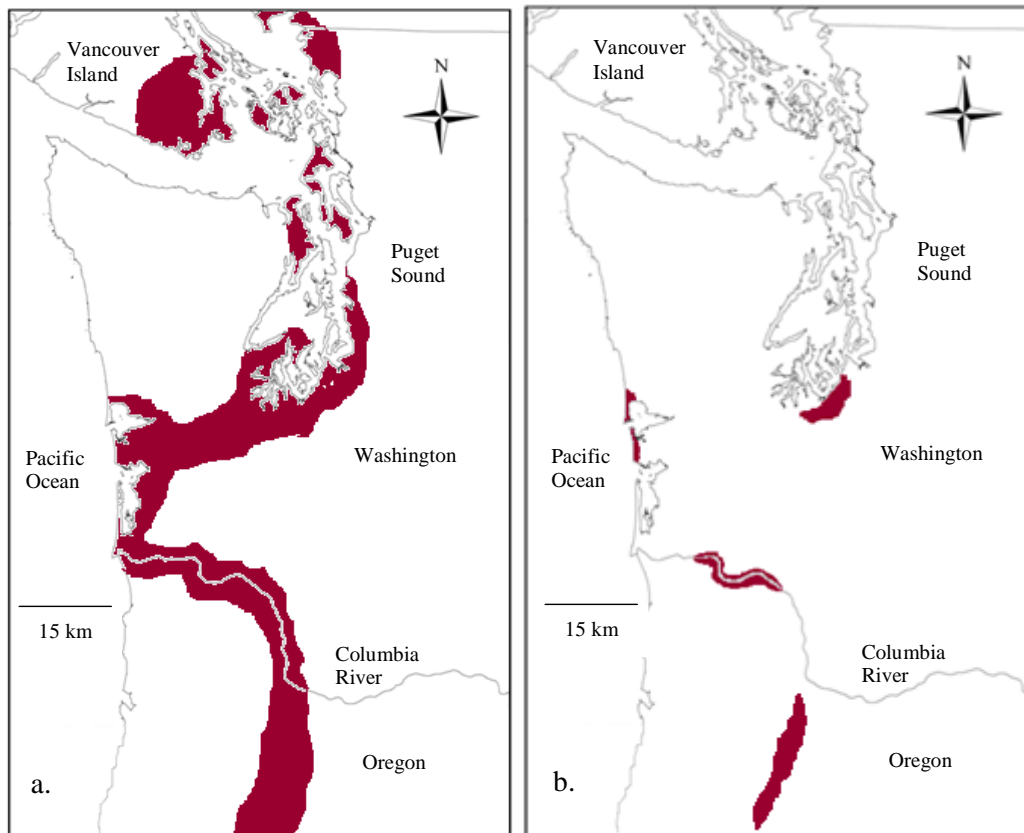


Figure 1a-b. Approximate historical distribution (a.) and current distribution (b.) of *E. a. strigata* (adapted from Gabrielson and Jewett 1940; Behle 1942; Rogers 2000; Altman 2003; Stinson 2005).

## POPULATION ESTIMATES AND THREATS

It is likely impossible to establish a reliable estimate of historic population size. As an example, it is unknown what proportion of the 170,000 acres of grassland soils in the Puget Sound supported suitable habitat (Chappell et al. 2001), or if the proportion changed or shifted due to dynamic abiotic factors (Stinson 2005). Today, the work of Altman (1999), Rogers (2000), Pearson (2003) and Pearson and Hopey (2004, 2005), indicate that there are approximately 800 *E. a. strigata* remaining, nearly half of which breed in the Willamette Valley (398 birds). One-third occupy habitats in the south Puget Sound (222 birds) while the remaining individuals are split nearly equally between the lower Columbia River and outer coast (68 and 86 birds, respectively).

As is true for many songbirds, habitat loss has, and will continue, to compromise the viability of *E. a. strigata*. Presently, grasslands west of the Cascade Mountains are among the most endangered ecosystem types in the region (Dunn and Ewing 1997; Rogers 1999, 2000). Across Washington and Oregon, grasslands composed predominantly of native species occupy just 3% of their pre-settlement range (Crawford and Hall 1997). In addition to the usual sources of habitat loss, such as urban development, fire suppression now severely threatens open habitat by allowing the establishment of both alien and native flora (Rogers 1999). In grasslands that do persist, encroachment by alien species such as *Agrostis tenuis* increase the density of vegetation beyond what is typically utilized for nesting (Beauschesne and Cooper 2003). This is especially problematic in the south Puget Sound, where most of the remaining habitat is within Fort Lewis Military Base, and has been managed under a policy of fire suppression for decades (Altman 1999).

The coastal nesting areas have also experienced a similar, albeit less extensive, contraction of suitable habitat. Even though there has been no systematic attempt to estimate the degree of landscape alteration, the loss of habitat to the invasion of non-native beachgrasses (*Ammophila spp.*) and erosion is likely considerable (Pearson and Altman 2005; Stinson 2005). European beachgrass was introduced as part of dune reclamation programs on the west coast of the United States beginning in the 19<sup>th</sup> century (Wiedemann 1987), and has increased as much as 574% over the past fifty years along portions of the Washington coast (Buell et al. 1995).

## **METHODS**

### **MODELING APPROACH**

Population Viability Analyses (PVA) are a collection of quantitative methods used to predict the likely future status of a population or collection of populations of conservation concern (Morris and Doak 2002). The earliest applications of PVA were the stochastic models of Shaffer (1981, 1983), who explored the consequences of grizzly bear (*Ursus arctos*) management in Yellowstone National Park. By that time, deterministic demographic analyses had been used for nearly a decade in the management of endangered species (Miller and Botkin 1974). Shaffer offered a new approach in population modeling when he developed a stochastic simulation that incorporated chance events (demographic and environmental stochasticity), producing probabilistic estimates of extinction risk (Shaffer and Samson 1985). PVA became a heuristic concept when Gilpin and Soule (1986) broadened it to include an examination of the synergism of interrelated risk factors through multivariate modeling. Since that time, the idea of PVA as a process of risk analysis has remained, where deterministic and stochastic factors are identified, risks associated with each are considered, and a model describing both factors and risks is developed (Beissinger and Westphal 1998).

Perhaps the most useful application of PVA, given the urgency and limited resources for managing declining species, is an evaluation of the likely outcomes of different management options on specific populations. Doing so provides a way to prioritize efforts in a manner that maximizes the likelihood of population persistence. (Pearson et al. 2008). Although some critics of PVA doubt its utility in conservation planning, alternative methods of making conservation decisions are often poorly adapted to account for uncertainty and less transparent about their reliability (Brook et al. 2000).

### **MODEL STRUCTURE**

I developed a stage- and space-structured demographic model to quantitatively investigate *E. a. strigata*'s viability in Washington. Only females were included in its formulation because I found no evidence of male limitation on female reproductive rates. I examined deterministic and stochastic versions; the latter of which allowed for year-to-year changes in survival rates due to fluctuations in the environment over time. Each matrix was parameterized according to a post-reproductive census as described in (McDonald and Caswell 1993): the population is censused in late summer after fledging but before any juvenile mortality or dispersal has occurred, and individuals must survive

to the next breeding season before reproducing. I distinguished two life-history stages: (a) juveniles (fledged individuals < 1-yr-old) and (b) adults ( $\geq$  1-yr. old), based on the age of sexual maturity (Fig. 2).

I used Lefkovitch stage-structured matrices, which provide a way of incorporating demographic data into a structured population growth model (Caswell 2001). Specifically, demographic rates determine a transition matrix  $\mathbf{A}$  containing the annual probabilities of surviving and reproducing. Multiplying the matrix by a vector  $\mathbf{n}_t$ , containing the distribution of individuals among stage classes in year  $t$ , gives the resulting distribution the following year. Successive years can then be modeled by iterating this equation. In their unmodified form, Lefkovitch matrices assume a single, well-mixed population lacking spatial structure and density-dependence, assumptions that I relax below. They also assume homogeneous probabilities of survival and reproductive success within each stage (Caswell 2001). All simulations were carried out using MATLAB (Mathworks 2008).

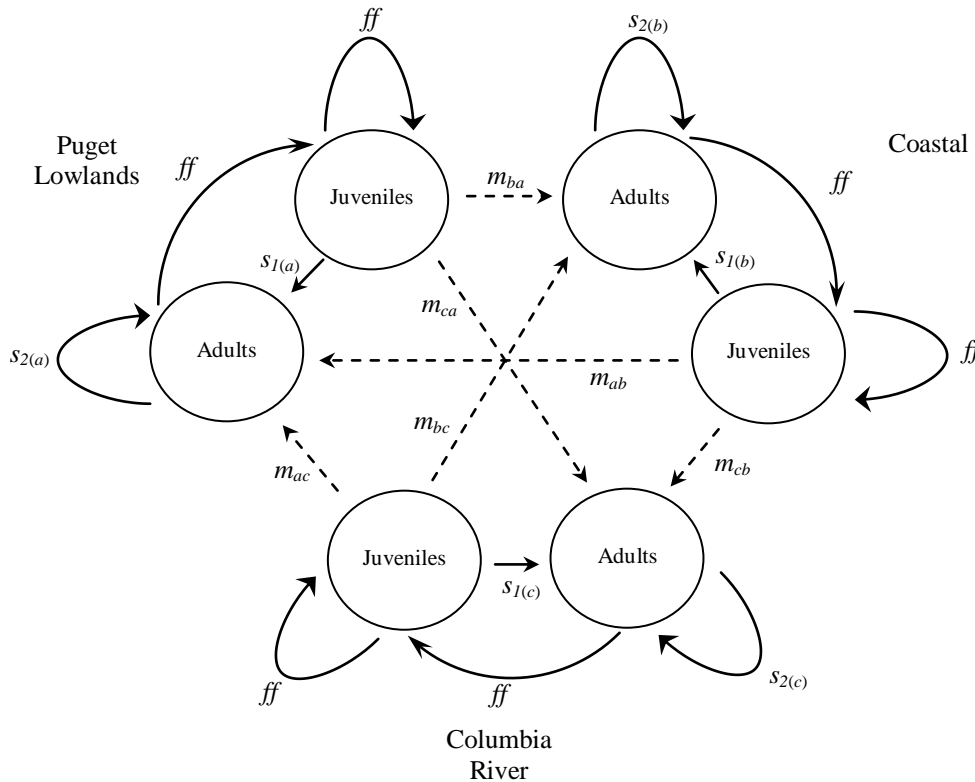


Figure 2. Simplified life cycle diagram of *E. a. strigata* used to guide the structure of the models developed in this paper. Fledglings survive to become adults according to a local juvenile survival probability,  $s_{1(i)}$ . Birds breed at one year of age according to a fecundity transition probability,  $ff$ , and survive thereafter according to a local adult survival probability,  $s_{2(i)}$ . The probability of juvenile dispersal is indicated by  $m_{ij}$  and represented by the dotted lines. Parameter abbreviations used in the models are presented in italics.

As was you will see below, the location of active nesting areas and the observed variation in local demography (see Parameters below) suggests the presence of at least three subpopulations, a violation of the assumption of homogeneity in unmodified Lefkovich matrix models. Specifically, both juvenile and adult survival depends on which subpopulation an individual occupies. Thus, I developed a spatially-structured matrix accounting for differences and spatial correlations in survivorship and movement between subpopulations. The matrix had the following form:

$$\begin{bmatrix} ff s_1(1 - m_{ba} - m_{ca}) & ff s_2(1 - m_{ba} - m_{ca}) & F_1 m_{ab} & F_2 m_{ab} & F_1 m_{ac} & F_2 m_{ac} \\ s_{1(a)} & s_{2(a)} & 0 & 0 & 0 & 0 \\ F_1 m_{ba} & F_2 m_{ba} & \mathbf{F_1(1 - m_{ab} - m_{cb})} & \mathbf{F_2(1 - m_{ab} - m_{cb})} & F_1 m_{bc} & F_2 m_{bc} \\ 0 & 0 & s_{1(b)} & s_{2(b)} & 0 & 0 \\ F_1 m_{ca} & F_2 m_{ca} & F_1 m_{cb} & F_2 m_{cb} & \mathbf{F_1(1 - m_{ac} - m_{bc})} & \mathbf{F_2(1 - m_{ac} - m_{bc})} \\ 0 & 0 & 0 & 0 & s_{1(c)} & s_{2(c)} \end{bmatrix}$$

where  $s_i$  is the survival rate of individuals in class  $i$ ;  $ff$  is the number of female fledglings per reproductive female; and  $m$  is the probability of juvenile dispersal,  $m_{ij}$ , from each site  $j$  to site  $i$ . The product  $\{ffs_i\}$  is the reproduction element ( $F_i$ ) of each stage-class. Note that the reproduction element for juveniles arises from the fact that birds in their first year of life begin the year as fledglings, but by the end of that year have produced fledglings of their own (Figure 1). The 2 x 2 sub-matrices (in bold) on the diagonal from the upper left to lower right corners represent the Puget Lowlands, Coastal, and Columbia River subpopulations (denoted by subscripts  $a$ ,  $b$ , and  $c$ , respectively).

I incorporated density-dependence in each of the two models using a population ceiling that limited the number of females. This approach was feasible for *E. a. strigata* due to its territorial behavior, which may limit the number of breeders as determined by the availability of habitat. The ceiling was calculated as two times the initial number of females in each subpopulation and was representative of the carrying capacity ( $K$ ) of each subpopulation. The ceiling was enforced only when the number of females exceeded  $K$ . If so, the model proportionally truncated individuals of both stages to the number allowed before proceeding with matrix-vector multiplication for the next time step.

## PRIMARY DATA SOURCES

At a minimum, realistic population modeling requires accurate estimates of vital rates for the population in question (Doak et al. 1994). To estimate survival rates for *E. a. strigata*, I relied heavily on mark-resight data gathered for the Washington Department

of Fish and Wildlife under the supervision of Dr. Scott Pearson. During the breeding seasons of 2002-2006, *E. a. strigata* were studied at seven sites in southwestern Washington, yielding data I used to estimate site- and stage-specific survival and dispersal rates (see Pearson et al. 2008 for description of sites). Estimates of fecundity were taken directly from Camfield et al. (2007). I relied on unpublished government reports (e.g. Pearson and Hopey 2004, 2005) for estimates of additional parameters.

### POPULATION SPATIAL STRUCTURE

Many of the seven sites studied by Pearson et al. (2008) exist in the form of clusters, where discrete nesting areas are situated close to each other. Observations of banded individuals suggest that among-area movements are common and that physically isolated habitats remain functionally connected. Thus, each study site could not be regarded as a distinct subpopulation. To delineate subpopulations, I created a 15-km buffer around each recorded nesting site and considered those sites whose buffers overlapped to constitute a single subpopulation. Consequently, the model contained 3 subpopulations (Fig. 3), where the minimum distance separating any two after applying the buffer was 70-km. I selected a 15-km buffer because *E. a. strigata* have a relatively high degree of site fidelity to previous nesting sites (Pearson et al. 2008). If breeders do change colonies within the same year, they are unlikely to move substantial distances. Inter-annual movements, which may involve longer distances, were modeled as dispersal.

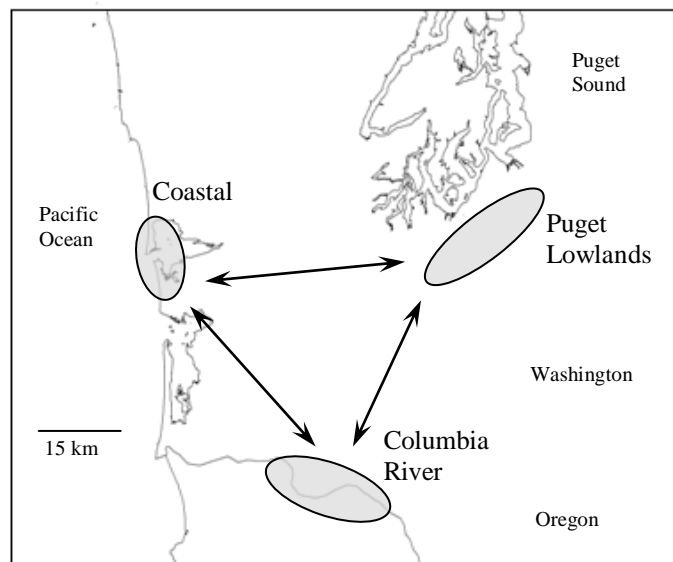


Figure 3. Spatial distribution of the subpopulations (shaded areas) making up the *E. a. strigata* population in Washington. Arrows indicate infrequent migration between subpopulations, the consequences of juvenile dispersal.



## PARAMETER ESTIMATES

### *Demographic Parameters*

I utilized the program MARK (White and Burnham 1999) to estimate annual rates of apparent survival and movement probabilities for juveniles and adults using the first-order Markovian multi-strata model (Brownie et al. 1993 and Hestbeck et al. 1991). This model is an extension of the Cormack-Jolly-Seber model (Cormack 1964, Jolly 1965, Seber 1965) that permits inclusion of categorical data (e.g. discrete subpopulations) in the encounter histories that can change during the life of an individual (Lebreton and Pradel 2002). The primary advantage of multi-strata models is that they yield estimates of apparent survival that are specific to each categorical state, while also estimating the probabilities of changing states (Sandercock 2006). I assumed that apparent survival in the interval time  $t$  to  $t + 1$  did not depend on the site at time  $t - 1$  (Brownie et al. 1993). I also assumed that individuals made site transitions near the end of each time interval and that individuals did not immigrate to sites outside of the study area (Sandercock 2006).

Apparent survival rates and movement probabilities were calculated using a reduced model where the probability of encounter was held constant (Table 1). Information-theoretic procedures using AICc's provided by Program MARK were utilized for model selection (Burnham and Anderson 2002). I used variance discounting to separate sampling variance from the process variance originating from demographic and environmental stochasticity (Burnham et al. 1987). In Program MARK, this procedure is fairly straightforward using random-effects models, which estimate and minimize sampling variation (White et al. 2001). Ideally, the result is an uncontaminated estimate of the environmental variance around each mean survival rate.

Dispersal in both models referred to the proportion of juveniles that transitioned from one subpopulation to another by the start of the following year (Bailey and Mock). This approach was especially feasible because the resighting probability in the mark-resight study was high (Pearson et al. 2008). For site transitions that had no observed dispersal ( $b \rightarrow a$ ;  $c \rightarrow a$ ,  $b \rightarrow c$ ;  $c \rightarrow b$ ;  $a \rightarrow c$ ), I arbitrarily assigned an annual movement probability of 0.0001 (Table 1). Fecundity rates were taken directly from Camfield et al. (2008), who estimated the number of female fledglings per female per year. Because this analysis did not provide site-specific estimates of fecundity, I assigned a uniform value across subpopulations (Table 1). Thus, the reproductive rate in each subpopulation was similar, with differences due only to the values of stage specific survival rates (see matrix formulation).

Table 1. Vital-rates used to parameterize a stage- and space-structured model for *E. a. strigata*.

<i>Parameter</i>	<i>Stochastic Form</i>	<i>Mean</i>	<i>Variance</i>
$s_{1(a)}$ = annual survivorship of juveniles, Puget Lowlands*	beta random variable (rv)	0.137	0.110
$s_{1(b)}$ = annual survivorship of juveniles, Coast*	beta rv	0.210	0.130
$s_{1(c)}$ = annual survivorship of juveniles, Columbia River*	beta rv	0.100	0.071
$s_{2(a)}$ = annual survivorship of adults, Puget Lowlands*	beta rv	0.444	0.163
$s_{2(b)}$ = annual survivorship of adults, Coast*	beta rv	0.714	0.116
$s_{2(c)}$ = annual survivorship of adults, Columbia River*	beta rv	0.272	0.179
$ff$ = number of fledglings produced per female, per year†	constant	0.910	
$m_{ab}$ = probability of juvenile moving from site <i>b</i> to <i>a</i> *	constant	0.0001	
$m_{ac}$ = probability of juvenile moving from site <i>c</i> to <i>a</i> *	constant	0.0001	
$m_{ba}$ = probability of juvenile moving from site <i>a</i> to <i>b</i> *	constant	0.1100	
$m_{bc}$ = probability of juvenile moving from site <i>c</i> to <i>b</i> *	constant	0.0001	
$m_{ca}$ = probability of juvenile moving from site <i>a</i> to <i>c</i> *	constant	0.0001	
$m_{cb}$ = probability of juvenile moving from site <i>b</i> to <i>c</i> *	constant	0.0001	

\* Source: Estimated from field data provided by S.F. Pearson.

† Source: Camfield et al. 2007.

### *Carrying Capacity, Initial Abundances, and Stage Distribution*

As described earlier, the carrying capacity of each subpopulation was defined as the maximum number of territories for breeding females, and was assumed to be two times the initial number of females in each subpopulation (Table 2). This assumption was largely arbitrary. There is little consensus on the average territory size of a nesting female, mostly because of the tendency of territory sizes to vary with habitat type and quality (Stinson 2005). Thus, I chose to set the carrying capacities at such levels where they would not qualitatively alter the conclusions of each model. However, I did test for the significance of this assumption, as described below in the sensitivity analysis. I estimated initial abundances of females in each subpopulation by dividing the numbers reported in Pearson and Hopey (2004, 2005) by two, assuming a one-to-one sex ratio. Because both the deterministic and stochastic models eventually converge to a stable-stage distribution, I distributed this total number to stage-classes by solving analytically for the dominant right eigenvector of each sub-matrix (Caswell 2001).

Table 2. Subpopulation-specific parameters used in simulations.

Subpopulation	Initial Abundance			Carrying Capacity
	Total <sup>a</sup>	Juveniles	Adults	
Puget Lowlands	111	53	58	222
Washington Coast	43	20	23	86
Columbia River	34	16	18	68

<sup>a</sup> Sources: Pearson and Hopey 2004, 2005

## DETERMINISTIC MODEL

The mean parameter values shown in Table 1 were used to construct the deterministic model. Because the dynamics of a population in a constant environment are captured by the iteration of a single transition matrix (Caswell 2001), modeling was a basic exercise in matrix multiplication. The deterministic growth rate  $\lambda_d$  (annual rate of population change) for each subpopulation was calculated numerically by projecting the number of individuals over 25 years (Caswell 2001). I quantified the dependence of the deterministic model's behavior on each parameter value by performing a two-step prospective perturbation analysis (Horvitz et al. 1997). First, I calculated sensitivity coefficients of  $\lambda_d$  to 5% changes (Mills et al. 1999) in: (1) the reproductive rate of females; (2) the survival rates of juveniles and adults, in each subpopulation; and (3) dispersal rates. This form of sensitivity analysis differs from analytical sensitivities based on eigenvalues (Caswell 2001) in that the parameters analyzed are not limited to the matrix elements and thus may include underlying vital rates and other parameters. I altered one parameter at a time, resetting each to its mean value before changing to the next and running the model again. The sensitivity coefficient of  $\lambda_d$  to each parameter was estimated as:

$$S_x^d = \frac{\lambda_{d,perturbed} - \lambda_{d,mean}}{x_{perturbed} - x_{mean}} = \frac{\Delta\lambda_d}{\Delta x};$$

where  $x$  is the parameter being perturbed. After calculating the  $S_x^d$  values for each parameter, deterministic elasticities were found using:

$$E_x^d = \frac{x}{\lambda_d} S_x^d.$$

Next, because the elasticity and sensitivity results are dependent on the vital-rate estimates used to make the matrix, inaccuracy in these estimates may have a substantial influence on the sensitivity results. The simplest way to explore the importance of uncertainty was to modify the method just described by simulating a set of random matrices where the parameters were drawn from a range of values for each vital-rate, assuming a uniform distribution. This is essentially a parametric bootstrap method to place confidence limits on the elasticities by asking how much of the variation in each growth rate is explained by the uncertainty in each vital-rate (Morris and Doak 2002). Minimum and maximum survival values were set to the 95% confidence limits calculated directly from the field data. The range of fecundity values was taken directly from Camfield et al. (2007).

## STOCHASTIC MODEL

One option for incorporating temporal variability is to simulate variation by randomly drawing from two or more projection matrices, each containing transition probabilities estimated over a separate time step (Morris and Doak 2002). There are two problems with this approach. First, data sets such as the one available for *E. a. strigata* do not allow the estimation of every entry in the matrix for all time steps or locations. This can result from poor experimental design or simply small sample sizes. If only the demographic data corresponding to a complete projection matrix is used, a great deal of information is lost (i.e. all data from sites or years that did not yield complete projection matrices). Second, the used of fixed matrices, each corresponding to an actual year of field work, enforces a very specific set of correlations in the variation of vital rates. Although these correlations exactly reflect the observed data, the use of fixed matrices prevents an exploration of the importance of correlation structure itself, apart from the variances represented among matrices (Doak et al. 1994).

To more flexibly simulate environmental stochasticity in survival rates, variation in the  $s_i(t)$ 's was represented as realizations of the beta distribution. The beta distribution is a family of continuous probability distributions confined to the interval [0, 1] and is appropriate for simulating survival rates, which are probabilities of binary events. I simulated random beta values with the means and variances specified in Table 1 using a method outlined in Morris and Doak (2002). This approach relies on the formula for the cumulative distribution function of the beta:

$$p = F(x|a, b) = \frac{1}{\beta(a, b)} \int_0^x t^{a-1} (1-t)^{b-1} dt;$$

where  $\beta(a, b)$  is the beta function built-in to MATLAB and  $a$  and  $b$  are transformations of the mean and variance, respectively, given by:

$$a = \bar{s}_i \left[ \frac{\bar{s}_i(1-\bar{s}_i)}{\text{var}(\bar{s}_i)} - 1 \right]; \text{ and } b = (1 - \bar{s}_i) \left[ \frac{\bar{s}_i(1-\bar{s}_i)}{\text{var}(\bar{s}_i)} - 1 \right].$$

For a beta distribution with parameters  $a$  and  $b$ , and a value  $p$  between 0 and 1, this function gives the probability,  $F(p|a, b)$ , that a random value chosen from the distribution will be less than or equal to  $p$ . In five steps: (1) I began with a uniform random number between 0 and 1 of  $F(p|a, b)$ ; (2) I chose a second random number  $x_1$  between 0 and 1 and calculated  $F(x_1|a, b)$ ; (3) if  $F(x_1|a, b)$  was greater than  $F(p|a, b)$ , I chose a random number  $x_2$  between 0 and  $x_1$ ; if  $F(x_1|a, b)$  was less than  $F(p|a, b)$ , I chose a random number  $x_2$  between  $x_1$  and 1; (4) I then set  $x_1 = x_2$  and recalculated

$F(x_i | a, b)$ ; (5) I repeated steps 3 and 4 until  $F(x_i | a, b) - F(p | a, b)$  was less than 0.01 which provided a good approximation of  $p$ . Rather than searching for a new value for each beta-distributed vital rate in each year, I began by storing a set of 99 beta values for each survival rate at the beginning of a simulation. These values were spaced uniformly by their cumulative distribution function values [ $F(p | a, b) = 0.01, 0.02, \dots, 0.99$ ]. I then drew random numbers for the  $F(p | a, b)$  value of each rate in each year and chose the stored rate with the closest  $F$  value. Morris and Doak (2002) found with a large number of stored values, this simplification does not influence the outcome of a stochastic simulation in any appreciable way and also provides the correct association to simulate correlated beta-distributed values.

To generate values of correlated beta random variables, I followed an approach developed in Gross et al. (1998) and expanded by Morris and Doak (2002). Because I lacked time specific estimates of fledgling production, I included only correlations between juvenile and adult survival within and across subpopulations, while treating fecundity as an independent parameter. Program MARK provided Pearson correlation coefficients for every pairwise combination of juvenile and adult survival, which were used to create a correlation matrix ( $\mathbf{C}$ ). This is a two-step process that uses correlated normal random variables to generate correlated survival rates with the beta distribution. I began with the correlation matrix estimated from the set of survival data. Taking the eigenvalues and right eigenvectors, I decomposed  $\mathbf{C}$  into two matrices:  $\mathbf{W}$  was a matrix with columns as the right eigenvectors of  $\mathbf{C}$ , and  $\mathbf{D}$  was a matrix with diagonal elements equal to the eigenvalues of  $\mathbf{C}$ . Then,  $\mathbf{C}^{1/2} = \mathbf{W} * \mathbf{D}^{1/2} * \mathbf{W}'$  where  $\mathbf{D}^{1/2}$  was a matrix with the square-roots of each eigenvalue on the diagonal and  $\mathbf{W}'$  was the transpose of matrix  $\mathbf{W}$ . Using  $\mathbf{C}^{1/2}$ , it was possible to take a set of uncorrelated standard normal values and convert them into a set of correlated normal values. With  $\mathbf{m}$  as a column vector of uncorrelated random values from a standard normal distribution,  $\mathbf{y} = \mathbf{C}^{1/2} * \mathbf{m}$  was a column vector containing now correlated standard normal variables, according to  $\mathbf{C}$ .

Next, by generating multiple  $\mathbf{m}$  vectors with different random values and then applying  $\mathbf{y} = \mathbf{C}^{1/2} * \mathbf{m}$  to each, I simulated a new vector of correlated values,  $\mathbf{y}_t$  for each year of a stochastic simulation. Then, I used these correlated standard normal values in each year  $\mathbf{y}_t$  to make a vector of corresponding values from the cumulative distribution function  $F_x$  for each standard normal. Abramowitz and Stegun (1964) provide an approximation for  $F_x$  that essentially computes the relative position of each random value along the range of possible values that a normal variable can exhibit. Finally, I used

these  $F_x$  values to find corresponding values for each of the survival rates by searching through the 99 beta values stored at the beginning of each simulation. This provided a good approximation of each pairwise correlation while preserving the cumulative distribution function of each beta random variable. This approach is solely phenomenological in that it describes the pattern of correlation evident in the data, but does not address any specific mechanism underlying that correlation (Doak et al. 1994).

I used stochastic simulations to estimate sensitivity and elasticity coefficients using the same method described for the deterministic model. In addition to the stage- and subpopulation-specific vital rates, I calculated sensitivity coefficients of  $\lambda_s$  to 5% changes in: (1) the variance of each simulated survival rate; and (2) the carrying capacity of each subpopulation. For stochastic simulations, I began with the subpopulation sizes shown in Table 2. Each simulation consisted of 10,000 replications for 25 years. I avoided projecting further into the future for two reasons: (1) the very low growth rates seen in the deterministic model made projections beyond this time frame irrelevant; and (2) given the results of Fieberg and Ellner (2000), the confidence intervals around the probability of extinction can easily encompass the entire range from zero to one as the time horizon approaches a century. Therefore, seeking to ensure the persistence of *E. a. strigata* by predicting and managing over an initial short time interval seemed more appropriate given the limitations of modeling.

### STOCHASTIC SIMULATIONS OF MANAGEMENT SCENARIOS

Using the same methods of the prospective perturbation analysis, I explored what levels of adult and juvenile survival and fecundity are required to yield estimates of  $\lambda_s \geq 1$  in each subpopulation. This procedure involved running a series of simulations with perturbed estimates of each of the three vital-rates ( $s_1$ ,  $s_2$ ,  $ff$ ) based on biologically realistic estimates producing a viable population of *E. a. articola*, a closely related subspecies of Horned Lark found in British Columbia (Camfield et al. 2007). First, I ran two simulations for each vital-rate increased by 10 and 20%. Next, I ran a set of simulations where I incrementally perturbed two vital rates in concert by 5 and 15%. A total of twelve simulations represented each possible combination of two vital rate manipulations ( $s_1 - s_2$ ;  $s_1 - ff$ ;  $s_2 - ff$ ) increased to both 5 and 15%. I avoided running simulations where the variance or spatial correlations between vital rates was perturbed. While both have serious implications for the persistence of small populations, it is rare that either can be altered through management (Morris and Doak 2002).

## RESULTS

### DETERMINISTIC MODEL

Projections of the deterministic model suggest that the three subpopulations will not sustain themselves for much longer than two decades (Fig. 4). Each declined to extinction by the twenty-fifth year regardless of the initial subpopulation size or stage-distribution. While the statewide population was projected to decline 39% per year ( $\lambda_d = 0.61$ ), the rate of decline of each subpopulation varied considerably (Table 4). Because the annual fecundity rate was set equal in each sub-matrix, disparities among local growth rates were attributable entirely to differences in survival and movement probabilities. The most striking result was how rapidly the Columbia River and Puget Lowlands subpopulations declined to extinction: neither persisted more than 10 years. Thus, for most of the projection, an extant statewide population was made possible only by the persistence of a small number of individuals (< 20) in the Coastal subpopulation.

I determined the sensitivity and elasticity of the deterministic model to small changes in vital rates as described previously. Sensitivity is defined as the absolute change in population growth rate per unit change in a parameter while all others are held constant (Wootton and Bell 1992). Elasticity measures the proportional response of population growth given a proportional change in a parameter, again, all other rates are held constant (Doak et al. 1994). Note that I calculated the sensitivities and elasticities of the measurable vital rates (Table 1), not the combinations of these rates that comprise the actual elements of the projection matrix.

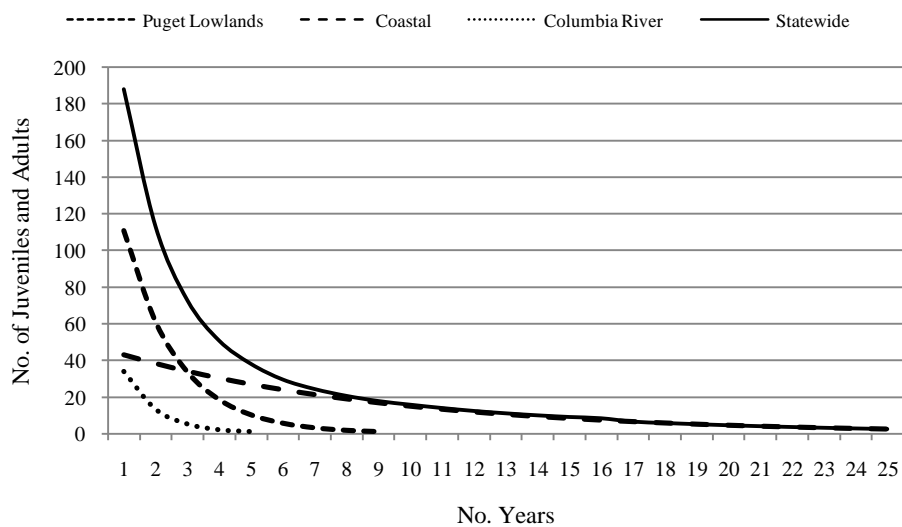


Figure 4. Projection in time of each of the subpopulations (deterministic model), with the statewide decline shown in bold.

The prospective perturbation analysis indicates that population growth is far more sensitive to changes in survivorship than to fecundity (Table 3). The maximum sensitivity always corresponded to the survival rates of adults in each subpopulation. The model was moderately sensitive to juvenile survival, and less sensitive to fecundity and juvenile dispersal. Also, the relatively small response of each local deterministic growth rate to changes in fecundity and the large sensitivity to changes in survival rates emphasizes the need to better quantify both juvenile and adult survival, given the low sample sizes currently available to calculate these rates.

Although elasticities aptly summarize the relative effects of small modifications in different demographic rates, they do not directly reflect how uncertainty in each rate may alter the reliability of the perturbation analysis. As described previously, I assessed the effects of this uncertainty by simulating selected vital rates from uniform distributions bounded by the 95% confidence interval around each mean estimate. The maximum local  $\lambda_d$ 's, given the uncertainty in survival and fecundity rates are shown in Table 4. The variation that did occur in each deterministic growth rate was largely generated by uncertainty in adult survival values, indicating that error in this rate was the most important in influencing the results of the sensitivity analysis.

Table 3. Local deterministic growth rates ( $\lambda_d$ ) and sensitivity and elasticity coefficients of vital rates (defined in Table 1). 95% confidence limits for elasticity values are shown in parentheses.  $s_{1(i)}$  = annual survivorship of juveniles;  $s_{2(i)}$  = annual survivorship of adults;  $ff$  = annual fecundity;  $m_{ba}$  = probability of juvenile moving from site  $a$  to  $b$ .

Parameter	Sensitivity	Elasticity (95% C.I.)
Puget Lowlands ( $\lambda_d=0.55$ )		
$s_{1(a)}$	0.809	0.201 (0.075, 0.437)
$s_{2(a)}$	1.000	0.799 (0.562, 0.924)
$ff$	0.122	0.201 (0.075, 0.437)
$m_{ba}$	-0.122	-0.025 (-0.153, -0.008)
Coastal ( $\lambda_d=0.89$ )		
$s_{1(b)}$	0.910	0.2143 (0.110, 0.493)
$s_{2(b)}$	1.000	0.7857 (0.508, 0.889)
$ff$	0.214	0.2143 (0.110, 0.492)
$m_{ba}$	0.091	0.031 (0.005, 0.168)
Columbia River ( $\lambda_d=0.41$ )		
$s_{1(c)}$	0.910	0.316 (0.053, 0.911)
$s_{2(c)}$	1.000	0.684 (0.088, 0.946)
$ff$	0.111	0.316 (0.053, 0.911)

Note: movement probabilities whose values were arbitrarily assigned are not included. Elasticity coefficients do not sum to 1 because, as described above, I calculated the sensitivities and elasticities of the underlying vital rates, as opposed to the elements of the projection matrix.



Table 4. Results of simulations to determine the sensitivity of local population growth to increases in vital rates. The maximum local  $\lambda_d$ , given the uncertainty in each parameter, is shown in boldface.

Vital Rate	Maximum vital rate value	Maximum potential value of local $\lambda_d$	Percentage variation in local $\lambda_d$ explained
Puget Lowlands			
$s_{1(a)}$	0.265	0.681	6
$s_{2(a)}$	0.740	<b>0.865</b>	90
$ff$	1.080	0.588	1
Coastal			
$s_{1(b)}$	0.455	<b>1.128</b>	21
$s_{2(b)}$	0.927	1.122	76
$ff$	1.080	0.946	3
Columbia River			
$s_{1(c)}$	0.327	0.516	9
$s_{2(c)}$	1.000	<b>1.091</b>	90
$ff$	1.080	0.440	0.1

More importantly, in simulations of the Coastal and Columbia River subpopulations, uncertainty in either juvenile or adult survival yielded growth rates in excess of one, thus encompassing increasing population dynamics. Consequently, I decided to rerun the deterministic model using estimates of survival pooled over all sites (projection shown in Fig. 5, survival values taken directly from Camfield et al. 2007). The time to extinction projected by the two models differed considerably, suggesting that, particularly for the Coastal subpopulation, the initial model is probably optimistic. Though it fails to account for spatial differences in demography, due to the imprecision generated by small sample sizes, the second projection may provide a more reliable summary of the probable statewide population decline.

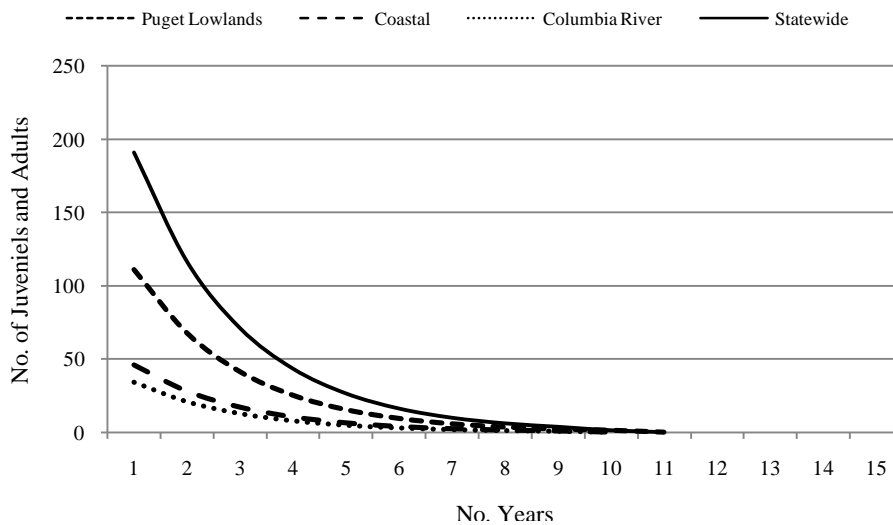


Figure 5. Projection in time of each of the subpopulations using pooled estimates of survival parameters. Juvenile survival in each subpopulation was set to 0.16; adult survival was set to 0.47 (taken directly from Camfield et al. 2007).

## STOCHASTIC MODEL

The stochastic model predicted population declines similar to those suggested by the deterministic model. While the average statewide and local growth rates were relatively unaffected by the addition of environmental stochasticity (compare Tables 4 and 5), it is clear that the addition of temporal variation tends to broaden the distribution of population sizes (Fig. 6). Although this distribution ultimately shrank as a result of the convergence on zero produced by extinctions of the Puget Lowlands and Columbia River subpopulations, over the first decade, much uncertainty was evident.

Table 5. Some results of the simulations (values from 10,000 replicates).

	Stochastic growth rate	Time of first extinction (yrs.)	Median time to extinction (yrs.)*	Extinction prob. at 25 yrs.
Statewide	0.58	13	17 (13-22)	<b>100</b>
Puget Lowlands	0.51	7	9 (7-12)	<b>100</b>
Coastal	0.83	13	17 (13-22)	<b>100</b>
Columbia River	0.39	3	4 (3-7)	<b>100</b>

\* Range shown in parentheses

Here, I show the full distribution of population trajectories (Fig. 's 6 & 7), rather than simply expressing the mean ending population size, because my concern was with the possibility of extinction or near extinction in any one realization of the future (i.e., any one simulated replication). Stochastic projections for each subpopulation are shown in Fig. 7. The Columbia River subpopulation was the first to decline to extinction, persisting on average less than five years. The Puget Lowlands also declined to extinction rapidly: by year 10 approximately 90% of replicates had resulted in extinction. The consequence of both early extinctions was startling: by the fifth year the statewide population had declined from 191 individuals to, on average, 35 individuals. As was the case with the deterministic model, the Coastal subpopulation was the most persistent (Table 5) and accounted for all individuals statewide beyond year 12.

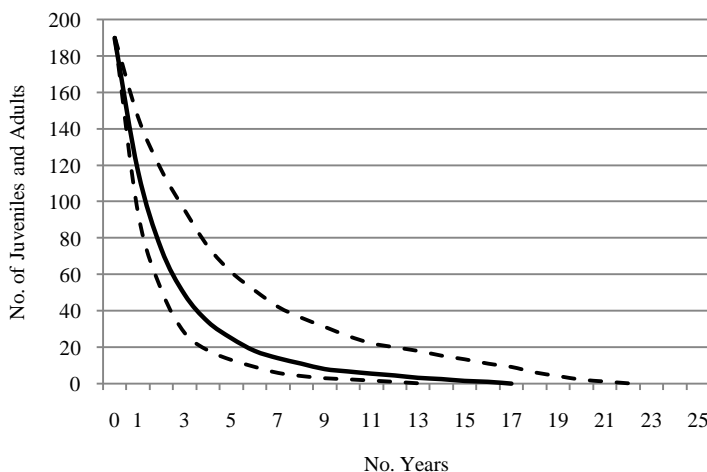
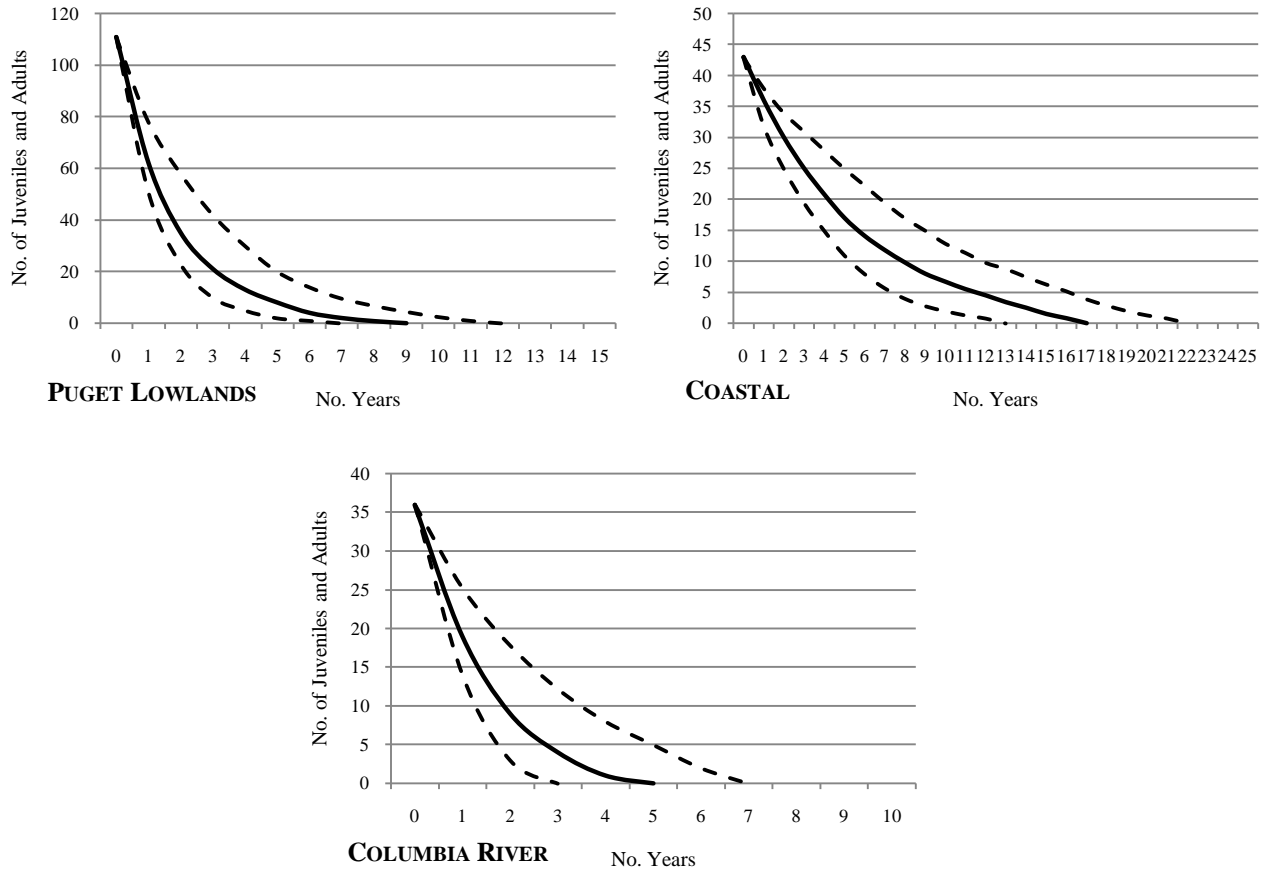


Figure 6. Stochastic projection in time of the statewide population, indicated by the solid line (mean values). The dashed lines represent the upper and lower bounds of the 95% confidence intervals around the mean estimate.

Figure 7. Stochastic projection in time of each of the subpopulations, indicated by the solid line. Again, the dashed lines represent the lower and upper bounds of the 95% confidence intervals around each mean estimate.



Sensitivity analysis of the stochastic model was qualitatively similar to the deterministic model, in that a given proportional change in adult survival caused a much larger effect on population growth than did changes in other parameters (Table 6). The model was moderately sensitive to fecundity, juvenile dispersal, and the variances of each survival rate. More striking, however, was the complete lack of sensitivity of each subpopulation to the local carrying capacity, strongly suggesting that each is demographically, rather than habitat, limited. In other words, the number of females needed to achieve population stability is not limited by the availability of nesting habitat.

As I did for the deterministic model, I reran the stochastic model using estimates of survival pooled over all sites. The statewide projection is shown in Fig. 8. Again, though failing to account for spatial differences in demography, this simulation suggests that the initial model is likely optimistic. By switching to the pooled estimates of survival, by the tenth year more than three-quarters of the 10,000 replicates had declined from 191 individuals to less than 5.

Table 6. Sensitivity and elasticity coefficients of local stochastic growth rates ( $\lambda_s$ ) to model parameters and variances.

Parameter	Sensitivity	Elasticity
<b>Puget Lowlands</b>		
$s_{1(a)}$	0.809	0.201
$s_{2(a)}$	0.961	0.740
$ff$	0.130	0.208
$m_{ba}$	-0.254	-0.051
variance of $s_{1(a)}$	-0.330	-0.035
variance of $s_{2(a)}$	-0.160	-0.011
<b>K</b>	<b>0.000</b>	<b>0.000</b>
<b>Coastal</b>		
$s_{1(b)}$	0.841	0.190
$s_{2(b)}$	1.020	0.812
$ff$	0.195	0.201
$m_{ba}$	0.236	0.029
variance of $s_{1(b)}$	-0.230	-0.015
variance of $s_{2(b)}$	-0.172	-0.012
<b>K</b>	<b>0.000</b>	<b>0.000</b>
<b>Columbia River</b>		
$s_{1(c)}$	0.881	0.204
$s_{2(c)}$	1.011	0.797
$ff$	0.103	0.217
variance of $s_{1(c)}$	-0.162	-0.021
variance of $s_{2(c)}$	-0.353	-0.048
<b>K</b>	<b>0.000</b>	<b>0.000</b>

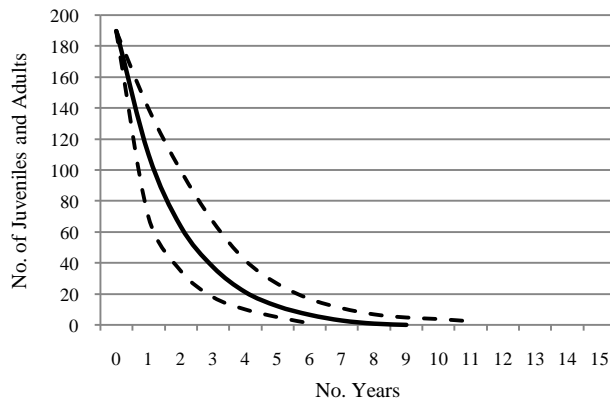


Figure 8. Stochastic projection of the statewide population, indicated by the solid line, using pooled estimates of survival from Camfield et al. 2007. The dashed lines represent the 95% confidence intervals around the mean estimate.

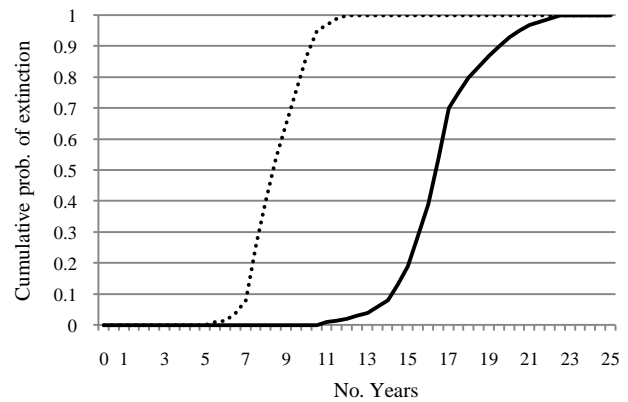


Figure 9. Cumulative extinction probability of the statewide population, according to the initial model (solid line) and model using pooled estimates of survival taken from Camfield et al. 2007 (dashed line).

## SIMULATION SCENARIOS

One advantage of modeling is that it allows simulation of hypothetical scenarios as a way to quantify the consequences of changes in the environment or in management strategies. As described previously, I considered different scenarios related to the effectiveness of management activities by simulating a priori positive changes in the demographic rates of each subpopulation. Local stochastic growth rates for two levels of independent vital-rate improvements are shown in Figure 10a-c. Clearly, the Coastal subpopulation is the most responsive to management. Modest increases (10%) of each demographic rate yielded growth rates of  $\lambda_s \geq 0.90$ . Though the subpopulation was still projected to decline to extinction, the increase in  $\lambda_s$  was sufficient to lengthen the median time to extinction by more than 5 years. A more optimistic improvement (20%) in adult survival was sufficient to yield an average estimate of  $\lambda_s > 1$ . Thus, it appears that increasing adult survival by 15-20% might, alone, be enough to halt declines of the Coastal subpopulation. The Puget Lowlands and Columbia River subpopulations were less responsive to independent manipulations. Even under the optimistic scenario (20% increases), the benefits realized were not encouraging. Still, the results of these large scale perturbations agree well with the sensitivity analysis; adult survival is of primary importance to *E. a. strigata*'s viability.

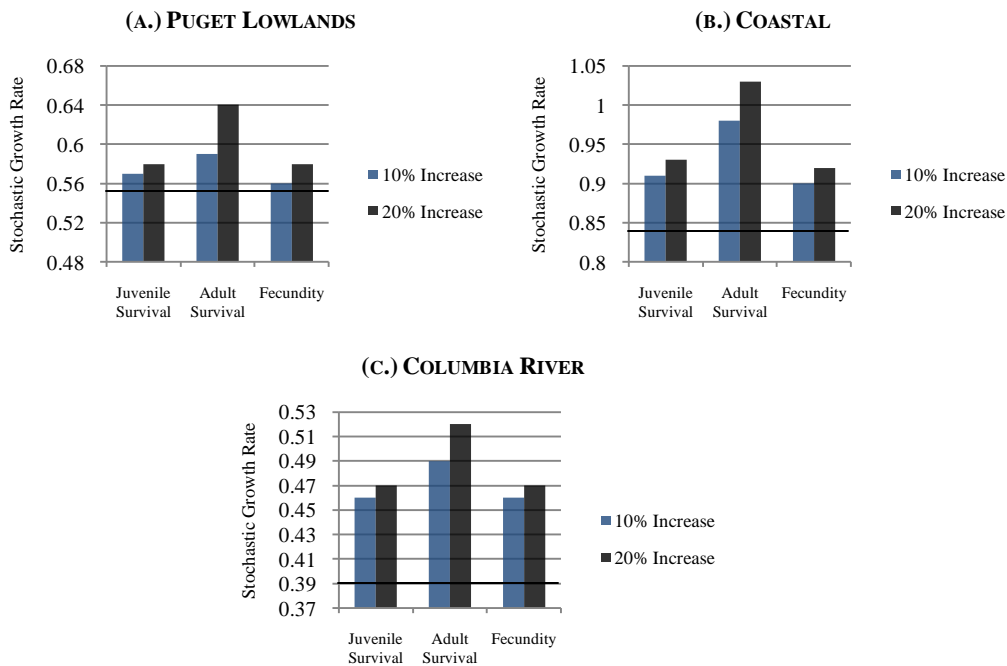


Figure 10. The stochastic growth rate ( $\lambda_s$ ) produced by independent perturbations of entries in the projection matrix. The baseline  $\lambda_s$  for each subpopulation is indicated by the solid line.

Local stochastic growth rates produced by four levels of simultaneous vital-rate improvements are shown in Figure 11a-c. Again, management activities targeting any demographic parameter were most effective when concentrated on the Coastal subpopulation. Any one of four scenarios (Fig. 11b) was sufficient to produce estimates of  $\lambda_s \geq 1$ . In contrast, the difficulty of achieving stable growth ( $\lambda_s = 1$ ) of the other two subpopulations reiterates the need for dramatic and timely management action.

Comparisons of the different scenarios suggest that the most effective strategy might be to target adult survival and fecundity in each subpopulation. An increase of these two vital rates by 15% would raise the statewide stochastic growth rate approximately 25%, and increase the median time to extinction by almost 10 years. Generally, smaller yet simultaneous increases yielded greater responses by each stochastic growth rate than independent perturbations, though both approaches had difficulty reversing the declines suggested by the baseline simulation.

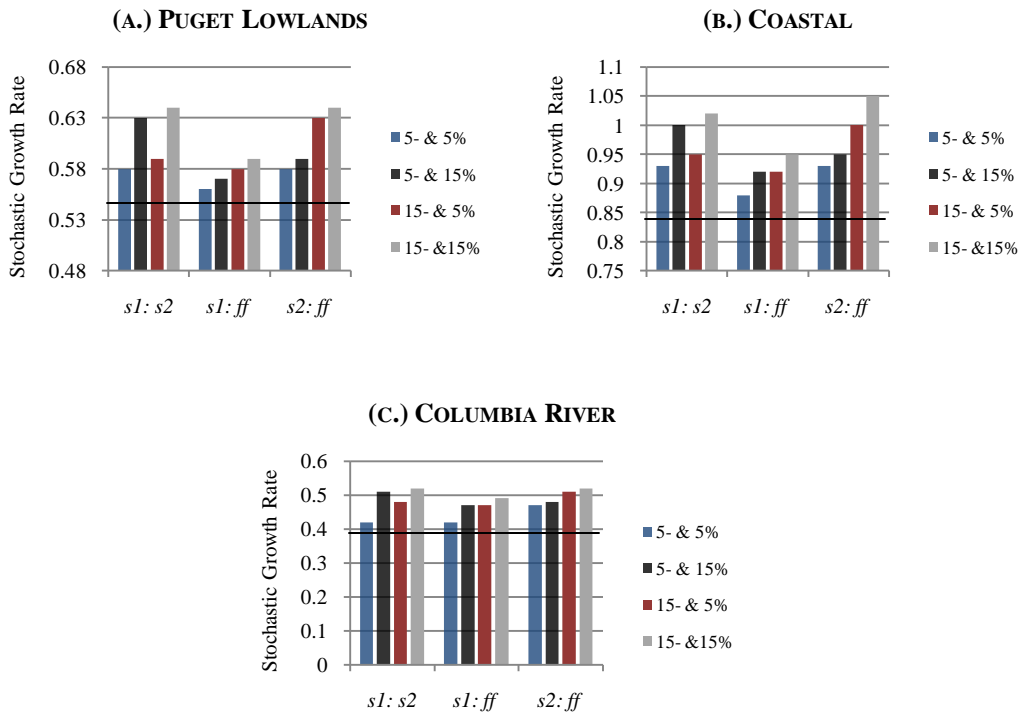


Figure 11. The stochastic growth rate produced by simultaneous perturbations of entries in the projection matrix. Increases shown in the legend indicate, respectively, how pairs of vital rates were manipulated. The baseline  $\lambda_s$  for each subpopulation is indicated by the solid line.

## DISCUSSION

Clearly, the subpopulations of *E. a. strigata* in Washington are in grave danger. My demographic analyses concur with the work of Pearson et al. (2008), who found that statewide, the population is declining by approximately 40% per year. Perhaps more interesting than this troubling conclusion is the way in which environmental stochasticity affects *E. a. strigata*'s prognosis. When variation in survival rates at levels estimated directly from field data was simulated, I obtained broad confidence limits for population sizes over the next decade. More often than not, environmental stochasticity had a cumulative tendency to hasten declines and shorten the median time to extinction. Thus, for *E. a. strigata*, and perhaps for many other endangered species (Menges 1992; Doak et al. 1994), models that fail to account for variability may mislead managers into thinking there is ample time to intervene before a population reaches zero, when in actuality extinction could be imminent, due simply to the inconsistencies of the environment.

In spite of the increasing number of empirical studies of population structure and dynamics, the need of adding realism to theoretical models is clear (Gaona et al. 1998). Intensive field work by Dr. Scott Pearson and others enabled me to avoid some usual limitations of population models, such as those resulting from the use of generic computer packages (e.g. VORTEX-Lacy 1993; RAMAS-Akçakaya and Ferson 1992; ALEX-Possingham and Davies 1995), which out of necessity contain a large number of assumptions and model behavior rather simplistically (Lindenmayer et al. 1995). For example, in many models of spatially-structured populations, similar values of demographic parameters are assigned across subpopulations (e.g., Akçakaya et al. 1995; Lindenmayer and Possingham 1996), making it difficult to identify disparities among local growth rates that are attributable to differential survival and fecundity.

Nonetheless, these models are not free of assumptions and limitations; and each should be considered carefully when evaluating the robustness of the results. First, assuming that yearly environmental states are independent of one another (i.e. no environmental autocorrelation) reduces the validity of the stochastic model if fluctuations are caused by systematic trends in environmental conditions, such as anthropogenic habitat deterioration or climate change. I also opted against simulating catastrophic events, which are a form of variation distinguished from environmental stochasticity by the magnitude of their effects on demography (Beissinger and Westphal 1998). They typically result in large population declines and greatly increase the chance of extinction (Mangel and Tier 1994). In the case of *E. a. strigata*, I saw little value in simulating such

events since the entire population would likely immediately go extinct, and would thus complicate the analyses of the simulated management scenarios.

Finally, some demographic parameters, notably the survival rates of the Coastal and Columbia River subpopulations, are derived from small sample sizes, and the sensitivity analysis indicates these rates could have a strong influence on population dynamics. The ability to develop accurate estimates of both the means and variance about vital rates is dependent on the number of years that a study has been conducted (Beissinger and Westphal 1998). Variance in growth rates does not begin to stabilize, if at all, until 8 to 20 years of data have been collected (Pimm 1991). Thus, the four annual transitions captured by the field study almost certainly do not represent the full range of environmental variation experienced by this subspecies.

The reality that such limitations and scarce data may compromise the validity of any viability analysis is unquestionable (Morris and Doak 2002). Indeed, a number of authors have raised important criticisms about applying quantitative population models to rare species (e.g. Boyce 1992, Beissinger and Westphal 1998). Thus, a sensible way to proceed is to consider relative risks (Beissinger and Westphal 1998), rather than basing decisions on absolute measures of viability. Knowing the exact, quantitative value of *E. a. strigata*'s growth rate is of lesser importance than considering a simple, more qualitative assessment of whether the population will tend to grow or decline. In this way, my confidence is strengthened by the consistent qualitative output across models. Despite the fact that quantitative predictions often disagreed, rarely were differences in the model structure or parameter values sufficient to yield estimates of  $\lambda > 1$ .

While the ultimate purpose of this research is to contribute to the conservation of *E. a. strigata*, providing managers with definite proposals of action is beyond the scope of this paper. Nevertheless, some reflections concerning conservation follow naturally from the results above. Although the current demographic rates for *E. a. strigata* warn of continued decline, my results suggest that preventable anthropogenic impacts may play a large role in that decline. Indeed, management to bolster adult survival and perhaps fecundity may foster some level of population stability. However, results of the sensitivity analysis also emphasize that some well-meaning management strategies, in particular efforts solely targeting fecundity, are unlikely to be either cost-effective or biologically sound. The simulation scenarios indicate that the effect of management activities will differ depending on location. For instance, increases of survivorship and fecundity only resulted in estimates of  $\lambda > 1$  in the Coastal subpopulation. By identifying



divergent local dynamics, management actions can be focused where they make the greatest contribution to the viability of the statewide population (Wootton and Bell 1992; Doak and Mills 1994; Gaona et al. 1998).

My work also provides information needed to prioritize future research efforts. For instance, the method I used to simulate the effect of management was quite crude; the results of such a model will be much more useful if conservation measures are evaluated empirically in terms of their impact on demographic parameters. Further information on the spatial and temporal variation in juvenile and adult survival are also especially important, given the low sample sizes currently available to calculate these rates and their importance in determining population growth. These data would decrease the uncertainty about vital rates, which contributed most of the imprecision to model results. Investigating the causes for relatively low fecundity, a comparatively small yet significant inhibitor of population growth, should also be a research priority, as should specific methods to improve each of the depressed vital rates.

In summary, I believe that the case of *E. a. strigata* is a hopeful one. Fortunately, the data needed to evaluate the viability of *E. a. strigata* is vastly better than that available for most endangered vertebrates. The subspecies has received state protection and may soon receive attention at the federal level. The Washington Department of Fish and Wildlife is eagerly investigating and implementing strategies that may improve demographic rates and my models demonstrate that management interventions may have positive effects for *E. a. strigata*. However, present legal protection aimed at averting the extinction of the subspecies is almost certainly inadequate. Both the deterministic and stochastic models demonstrate that complacency is ill-advised; decisive action to quickly improve demographic rates is needed, given the consistent qualitative conclusions across models and the uncertainty inherent in predictions of future population trends.

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