INTERACTIVE EFFECTS OF PREY AND p,p'DDE ON BURROWING OWL POPULATION DYNAMICS

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Abstract. We used population models to explore the effects of the organochlorine contaminant p,p'DDE and fluctuations in vole availability on the population dynamics of Burrowing Owls (*Athene cunicularia*). Previous work indicated an interaction between low biomass of voles in the diet and moderate levels of p,p'DDE in Burrowing Owl eggs that led to reproductive impairment. We constructed periodic and stochastic matrix models that incorporated three vole population states observed in the field: average, peak and crash years. We modeled varying frequencies of vole crash years and a range of impairment of owl demographic rates in vole crash years. Vole availability had a greater impact on owl population growth rate than reproductive impairment if vole populations peaked and crashed frequently. However, this difference disappeared as the frequency of vole crash years declined to once per decade. Fecundity, the demographic rate most affected by p,p'DDE, had less impact on population growth rate than adult or juvenile survival. A life table response experiment of time-invariant matrices for average, peak and crash vole conditions showed that low population growth under vole crash conditions was due to low adult and juvenile survival rates, whereas the extremely high population growth under vole peak conditions was due to increased fecundity. Our results suggest that even simple models can provide useful insights into complex ecological interactions. This is particularly valuable when temporal or spatial scales preclude manipulative experimental work in the field or laboratory.

Keywords: Athene cunicularia*, Burrowing Owl, DDE, elasticity, interactive effects, matrix population model, multiple stressors, population level risk assessment, prospective analysis.*

INTRODUCTION

Contaminants have long been recognized as a threat to ecological systems but assessing risk to levels of biological organization above that of the individual has been systematically undertaken only recently (e.g., Newman and Jagoe 1996, Kammenga and Laskowski 2000, Pastorok et al. 2002). Despite this increasing attention, it is still far from obvious how to assess the effects of pollutants on wild populations. Methods that are highly successful at predicting risk to individuals do not adequately predict population-level effects (Kammenga et al. 1996, Forbes and Calow 1999, Stark and Banks 2000). They also rarely account for the effects of interacting stressors, the variable nature of exposure in free-living organisms, and the spatial distribution of contaminants.

A major challenge in determining the impacts of contaminants on populations is the frequent exposure of organisms to multiple contaminants, and the resulting non-linear interactions among contaminants (Birnbaum et al. 1985, Davis and Safe 1988). Anthropogenic stressors such as persistent organic pollutants may also interact non-linearly with natural stressors. Contaminants can interact with environmental factors such as food availability, density dependence, or predation to produce population responses that differ sharply from those demonstrated by populations exposed to only the contaminant. For example, toads in carbaryl-treated ponds had higher survival than toads in untreated ponds, apparently because their algal food source underwent competitive release from zooplankton in the presence of carbaryl (Boone and Semlitsch 2002). In another study, toxicity of nitrate fertilizer interacted with low pH in ponds and UV B radiation to reduce the survival of frogs (Hatch and Blaustein 2000). Organism density also has been shown to have potentially dramatic effects on the impact of a contaminant on a population (Linke-Gamenick et al. 1999, Boone and James 2003, Forbes et al. 2001, Forbes et al. 2003).

Because of this complexity, at least three questions must be addressed before ecological and population-level impacts can be assessed. First, what conditions or factors interact with contaminants and influence how toxic effects are expressed? Second, are the interactions synergistic, antagonistic, or additive? Third, are the conditions persistent, or, if intermittent, at what frequency do they occur?

Assessment of the population-level effects of contaminants is difficult because contaminant effects can vary through time as a result of variation in the contaminant itself or through variation in an interacting contaminant or stressor (Keith and Mitchell 1993, Gervais and Anthony 2003, Hatch and Blaustein 2003). The appropriate spatial and temporal scales often preclude data collection of sufficient scope or duration to directly estimate effects in the field. Experiments are difficult for the same reasons, in addition to ethical constraints on deliberately applying persistent contaminants to the environment. A feasible alternative is to combine information from multiple sources into an estimate of the effect on the population. Demographic modeling offers the opportunity to integrate the effects of multiple stressors acting on different aspects of an organism's life history and evaluate the impact of those stressors at the population level.

We used population modeling to explore the potential effects of a contaminant acting synergistically with a natural stressor on Burrowing Owl (*Athene cunicularia*) population dynamics. This investigation was motivated by study of a Burrowing Owl population that lived in an intensive agricultural matrix of the San Joaquin Valley of California (Gervais et al. 2000, Gervais et al. 2003, Gervais and Anthony 2003). Owls in the study population foraged in agricultural fields that were treated with pesticides highly toxic to birds (Gervais 2002, Gervais et al. 2003). Individual females had sufficient body burdens of contaminants to lay eggs containing up to 33 $\mu g/g$ wet weight of organochlorine contaminants. The most prevalent contaminant was p,p'DDE, the para, para isomer of dichlorodiphenyldichloroethylene (Gervais and Anthony 2003), the primary metabolite of DDT. Although egg concentrations of contaminants indicated that all females maintained elevated concentrations of p,p'DDE, only a few owls were associated with highly contaminated eggs and this number varied from year to year (Gervais and Anthony 2003). Despite evidence of exposure to agricultural chemicals and persistent organochlorine residues, no direct relationships between contaminants and survival or fecundity were found (Gervais et al. 2003, Gervais and Anthony 2003).

However, there was a relationship between low rodent biomass in the diet during years when rodent prey was scarce and reduced fecundity in individual owls with moderately contaminated eggs (Gervais and Anthony 2003). This synergistic effect was not present in years when rodents were more common in the owls' diet. The annual proportion of owls in the population laying eggs with levels of p,p'DDE associated with impaired reproduction varied widely, from none of the eggs collected to all of them (Gervais and Anthony 2003). In addition, rodent populations appeared to undergo dramatic changes in density on a year to year basis. Assessing the population-level consequences of the observed synergy between contaminants and reproductive success will require consideration of a range of environmental conditions and contaminant levels.

In this paper, we examine the effects of organochlorine contaminants and fluctuations in prey availability on the dynamics of this Burrowing Owl population. Our primary goal was to determine whether contaminant level exposures such as those that we documented could impair population-level processes. We evaluated the effect of varying the frequency and intensity of contaminant impacts on reproduction and survival using deterministic and stochastic population models. We also performed prospective and retrospective analyses to investigate how changes in demographic rates affected overall population growth rate. Our secondary goal was to evaluate the consistency of the conclusions from different model analyses given the uncertainty arising from incomplete data. Finally, we explore the utility of these types of analyses in assessing risk to populations.

STUDY POPULATION

The study population consisted of 63-85 resident breeding pairs of Burrowing Owls living on Naval Air Station (NAS) Lemoore (36°18'N, 119°56'W), 50 km southwest of Fresno, California USA. The owls nested in burrows along the runway easements and in adjacent fallow fields. The landscape was primarily intensive row crop agriculture. Dominant crops were cotton and alfalfa, with lower proportions of tomatoes, safflower, and other crops. The region has been treated with a wide variety of agricultural pesticides in recent years (California Department of Pesticide Regulation 1998, 1999).

Organchlorine chemical analysis of whole egg contents from owls nesting in this area between 1996 and 2001 (n=92) detected persistent organochlorine contaminants, most notably p,p'DDE (Gervais et al. 2000, Gervais and Anthony 2003). Overall, eight percent of the eggs contained organochlorine residues at concentrations sufficient to cause reproductive harm in other avian species (Gervais et al. 2000). On an annual basis, contaminant levels of concern were found in none to all of the eggs sampled that year (Gervais and Anthony 2003).

In the Lemoore population, there was a relationship between low rodent biomass in the diet and reduced fecundity in owls with moderately contaminated eggs (Gervais and Anthony 2003). Burrowing Owls with $> 4\ \mu g/g$ p,p'DDE in their eggs and a dietary biomass of rodents of $< 3g$/pellet raised only 2.0 owlets to fledging (95% CI: 0.7 - 3.2, n=5), whereas owls that did not meet these two conditions raised 3.8 owlets to fledging (95% CI: 3.1 - 4.5, n=62; Gervais and Anthony 2003), a 47% reduction in fecundity. Egg contaminant levels fluctuated widely from year to year but in general only a few eggs were highly contaminated (Gervais and Anthony 2003). The annual percentage of owls with moderate contaminant residues and low vole biomass in their diet ranged from none to 15% between 1996 and 2001. The exception was 1996, when all egg samples exceeded the threshold of 4 $\mu g/g$ p,p'DDE, but specific diet information was not available for this year (Gervais et al. 2000). Overall reproduction in the population could have been halved in 1996. However, it is not clear whether this could have reduced population growth rate.

POPULATION DYNAMICS

Burrowing Owls are relatively short-lived; in the Lemoore population they were rarely recorded as living more than four years (J. A. Gervais and D. K. Rosenberg, unpublished data). They breed at one year of age and are capable of producing up to twelve fledglings per nesting attempt (Haug et al. 1993). We constructed a two-stage, female-only matrix model, based on a post-breeding census (Fig. 1). Juveniles were considered to be age 0-1 year and adults were aged > 1 year. Survival differed between adults and juveniles. Because this was a post-breeding census, juveniles breed when they enter the adult class, we assumed reproduction of adults and juveniles entering the adult class was equal. Although Burrowing Owls have been known to produce two broods in a year (Gervais and Rosenberg 1999), this is rare and we did not account for it in our model. The annual projection matrix is

$$\mathbf{A} = \begin{pmatrix} s_j b & s_a b \\ s_j & s_a \end{pmatrix} \tag{1}$$

where s_j is juvenile survival probability, s_a is adult survival probability, and b is fecundity. All analyses were conducted in MATLAB.

Estimates of demographic rates

We parameterized transition matrices for four years (1997-2000; Table 1) from data collected at Lemoore. Observations of individually marked birds were used to estimate survival rates (the probability of survival from time t to $t+1$) and capture probabilities (the probability a marked individual that is alive at time t is encountered at time t) using the mark-recapture methods in program MARK (White and Burnham 1999). An *a priori* set of modified Cormack-Jolly-Seber models that examined survival rates and capture probabilities in relation to age, gender and time were developed based on field experience and perceptions about likely sources of variation in these parameters. For a thorough introduction to survival estimation using mark-recapture techniques see Williams et al. (2001), and for detailed methodology including the full set of models considered see Gervais (2002). Models were compared using Akaike's Information Criterion, AIC$_c$, adjusted for small sample bias (Burnham and Anderson 2002). AIC$_c$ ranks models based on optimization of fit and precision so that the best approximating model in the set provides the most parsimonious explanation ofthe data. Estimates of adult female and juvenile survival were taken from the model with the most support based on AIC$_c$ which allowed survival to vary by gender, year, and age in a linear combination, and allowed recapture probability to vary by gender. Survival is assumed to be underestimated due to emigration, which we could not estimate, but our focus here is on relative rather than absolute population effects. We hereafter refer to survival as apparent survival. Fecundity was estimated from standardized nest watches (Gervais 2002). This is also underestimated because of the difficulty in detecting all young in burrow-nesting species (Gorman et al. 2003). This bias is likely to be year-specific, as environmental conditions affect emigration rates and the detectability of young owls, but measures of this bias were not available. Fecundity is expressed as female young produced per female, assuming an even gender ratio of young at birth.

Time-specific demography

Observed demographic rates were highly variable among the four years of the field study (Table 1). We examined the dynamics that would be produced if the demographic rates observed in a single year were to remain constant over a long period of time, evaluating this for each of the four years separately. We refer to the projection matrices for 1997, 1998, 1999 and 2000 as $\mathbf{A}_{97}$, $\mathbf{A}_{98}$, $\mathbf{A}_p$, and $\mathbf{A}_c$, respectively. High demographic rates were observed in 1999 in response to high densities of California voles (*Microtus californicus*), which were a primary food source (Gervais 2002, Gervais and Anthony 2003). We designate this as a peak year. A vole population crash in the following year (2000) was accompanied by extremely low demographic rates (Table 1), and we designate this as a crash year.

Linear time-specific dynamics are described by the population projection equation $\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t)$, where $\mathbf{n}(t)$ is the population vector at time t. We used the dominant eigenvalue, λ, of $\mathbf{A}$ as a measure of the long-term population growth rate. We calculated the stable stage distribution and reproductive value as the right and left eigenvectors, $\mathbf{w}$ and $\mathbf{v}$, respectively, of $\mathbf{A}$ that correspond to λ (Caswell 2001). To evaluate potential effects of reductions in the demographic parameters (i.e. s_a, s_j and b) that might result from pesticide contamination we calculated the elasticity of λ to changes in the parameters (i.e. the proportional change in λ resulting from a proportional change in a parameter). The elasticity of λ to change in a parameter θ is (Caswell 2001)

$$e_\theta = \frac{\theta}{\lambda}\frac{\partial\lambda}{\partial\theta} = \frac{\theta}{\lambda}\sum_{i,j}\frac{\partial\lambda}{\partial a_{ij}}\frac{\partial a_{ij}}{\partial\theta} \tag{2}$$

where a_{ij} is the ij^{th} entry of $\mathbf{A}$.

We used a life table response experiment (LTRE) analysis (*sensu* Caswell 1996) to determine contributions of the parameters to differences in λ among years (Caswell 1996, Levin et al.

1996, Caswell 2001). We classified the projection matrices as average ($\mathbf{A}_{97}$ and $\mathbf{A}_{98}$), peak ($\mathbf{A}_p$) and crash ($\mathbf{A}_c$) conditions based on vole availability as a food source. We used the mean of the two average matrices as the reference matrix, $\mathbf{A}_a$. We estimated contributions of the parameters to the change in λ between average and peak conditions and between average and crash conditions. Let $\lambda^{(a)}$ and $\lambda^{(p)}$ be population growth rates under conditions in average and peak years, respectively. Effects of the parameters on the change in λ are measured relative to $\mathbf{A}_a$ using the first-order linear approximation:

$$\lambda^{(p)} - \lambda^{(a)} \approx \sum_i \left(\theta_i^{(p)} - \theta_i^{(a)}\right) \frac{\partial \lambda}{\partial \theta_i}\bigg|_{(\mathbf{A}_p + \mathbf{A}_a)/2} \tag{3}$$

where $\theta_i^{(a)}$ is the i^{th} parameter in the matrix $\mathbf{A}_a$. The i^{th} term in the summation is the contribution of differences in θ_i in $\mathbf{A}_a$ and $\mathbf{A}_p$ to the difference in population growth rate. The contributions to the change in λ between average and crash years ($\lambda^{(a)}$ and $\lambda^{(c)}$) were calculated in the same way.

Growth rate projections from deterministic models assume that the population has reached the stable stage distribution. We evaluated the transient dynamics of the time-invariant model using the methods of Fox and Gurevitch (2000).

Modeling frequency and intensity of contaminant effects

Time-specific analyses characterize the environments (average, peak, and crash vole conditions) in terms of their ability to support owl population growth, but they tell us only what would happen if a particular set of conditions remained constant over time. In reality the owls experience some sequence of these conditions, causing owl populations to fluctuate over time. A peak vole population year is generally followed by a population crash the next year, and this two-year sequence is separated by some number of years with intermediate vole abundance. The number of intervening years may vary, depending on whether vole populations cycle every two years, less often, or whether they fluctuate in a more unpredictable fashion (Pearson 1966, Garsd and Howard 1981).

Because p,p'DDE contamination affects owl demographic rates in years when owls consume fewer voles (Gervais and Anthony 2003), the effects of p,p'DDE contamination on population dynamics will depend on i) the frequency of vole population crashes; ii) the arrangement of average, peak and crash years within the cycle, and iii) the level of impairment of a demographic rate under crash conditions. Evaluating contaminant effects on owl population dynamics requires incorporating this periodicity in a population model. The matrices representing owl demographics under different scenarios of vole availability ($\mathbf{A}_a$, $\mathbf{A}_p$ and $\mathbf{A}_c$) can be combined in either a periodic model, in which different conditions are assumed to occur in a repeated deterministic sequence, or in a stochastic model, where each set of conditions has a particular probability of occurring at each time step. The effects of the frequency of vole crashes on population growth are difficult to predict *a priori*. Because peak and crash years are linked, reducing the frequency of vole population crashes reduces the frequency of both good years (the best conditions) and bad years (the worst conditions). This attenuates their effects, and conditions in the intervening years have increasing influence on population growth.

Deterministic periodic analyses

To model cyclic vole population crashes, we constructed a periodic model with an annual time step. The periodic model specified a repeated deterministic sequence of average ($\mathbf{A}_a$ as defined above), peak ($\mathbf{A}_p$) and crash years ($\mathbf{A}_c$) that corresponded to average, peak and crash vole abundance, respectively. A peak year was always followed by a crash year and this combination of years was separated by a specified number of average years. The dynamics over time were modeled as

$$\mathbf{n}(t+y) = \mathbf{A}_c\,\mathbf{A}_p\mathbf{A}_a^k\mathbf{n}(t) \tag{4}$$

where k is the number of average years occurring in a cycle. The total number of years in the cycle is $y = k + 2$, the number of average years plus a peak year and a crash year. We calculated the annual long-term population growth rate (λ_{pd}) as the y^{th} root of $\lambda_{\mathbf{B}}$, the dominant eigenvalue of the periodic matrix product $\mathbf{B} = \mathbf{A}_c\,\mathbf{A}_p\mathbf{A}_a^k$,

$$\lambda_{pd} = \lambda_{\mathbf{B}}^{\frac{1}{y}} \tag{5}$$

We investigated the effects of both the frequency and intensity of impairment associated with p,p'DDE. Vole populations at Lemoore peaked and crashed only once between 1996 and 2001 and the average length of vole cycles in this region is unknown. We therefore investigated a range of plausible vole cycle lengths. To explore the effects of the frequency of vole crash years we varied the interval between vole crashes from three to twelve years by varying k from 1 to 10. We explored the effect of contaminant intensity by independently reducing each demographic parameter by 0% to 50% in vole crash years. All eggs sampled in 1996 contained levels of contaminants that could have caused 50% reproductive impairment under low rodent conditions. Although only reproduction appeared to be impaired by p,p'DDE (Gervais and Anthony 2003), we examined the effects of perturbations of both reproduction and survival, altering each demographic rate independently. This allowed us to explore the potential consequences of an interactive effect with other toxicants, such as a carbamate insecticide (e.g., James and Fox 1987) that do affect survival.

For each combination of cycle length and intensity of impairment, we calculated λ_{pd} and the elasticities of λ_{pd} to the demographic parameters. As in the time-specific analyses, the elasticities estimate the effect on λ_{pd} of potential reductions in the demographic parameters.

The elasticities of λ_{pd} to the parameters in a periodic model depend on how a parameter θ affects the matrices $\mathbf{A}_c$, $\mathbf{A}_p$, and $\mathbf{A}_a$. The elasticity of $\lambda_{\mathbf{B}}$ for the periodic cycle $\mathbf{B}$ to θ was calculated as

$$e_\theta^{\lambda_{\mathbf{B}}} = \frac{\theta}{\lambda_{\mathbf{B}}}\frac{\partial\lambda_{\mathbf{B}}}{\partial\theta} = \frac{\theta}{\lambda_{\mathbf{B}}}\left[\sum_{i,j}\frac{\partial\lambda_{\mathbf{B}}}{\partial a_{ij}^{(c)}}\frac{\partial a_{ij}^{(c)}}{\partial\theta} + \sum_{i,j}\frac{\partial\lambda_{\mathbf{B}}}{\partial a_{ij}^{(p)}}\frac{\partial a_{ij}^{(p)}}{\partial\theta} + k\sum_{i,j}\frac{\partial\lambda_{\mathbf{B}}}{\partial a_{ij}^{(a)}}\frac{\partial a_{ij}^{(a)}}{\partial\theta}\right] \tag{6}$$

where the superscripts in parentheses denote the annual matrix (Caswell and Trevisan 1994, Lesnoff et al. 2003). The elasticities of λ_{pd} to $a_{ij}^{(x)}$, $\frac{\partial\lambda_{\mathbf{B}}}{\partial a_{ij}^{(x)}}$ in (6) were calculated according to equation 13.40 in Caswell (2001). Because $\lambda_{\mathbf{B}}$ describes growth over a cycle of $y = k + 2$ years, the elasticities were converted to an annual basis as

$$e_\theta^{\lambda_{pd}} = \frac{1}{y}\left(\lambda_{\mathbf{B}}^{\frac{1-y}{y}}\right)\frac{\theta}{\lambda_{\mathbf{B}}}\frac{\partial\lambda_{\mathbf{B}}}{\partial\theta} \tag{7}$$

We used a Monte Carlo approach to generate the standard error of λ_{pd}. We drew the survival parameters from beta distributions to constrain the values to between 0 and 1, and the reproduction parameter from a gamma distribution to impose a lower bound of 0. All parameters were drawn independently using the means and standard errors given in Table 1, a matrix constructed, and λ_{pd} calculated. This process was repeated 10,000 times. The resulting distribution of λ_{pd} describes the uncertainty in the estimate of λ_{pd} arising from uncertainty in the parameters.

The population growth rate and elasticities are asymptotic properties of the model. The rate of convergence to these asymptotic values and any oscillations prior to convergence are governed by the subdominant eigenvalues. For a two-stage model, as in our case, convergence is determined by the damping ratio, ρ,

$$\rho = \frac{\lambda_{pd(1)}}{\left|\lambda_{pd(2)}\right|} \tag{8}$$

where $\lambda_{pd(1)}$ and $\lambda_{pd(2)}$ are the dominant and sub-dominant eigenvalues of $\mathbf{B}$, respectively. Convergence is more rapid for larger ρ. We calculated ρ as a measure of transient effects in the periodic model.

Stochastic analyses

Vole cycles are not precisely periodic in this region. The interval between a crash year and the next peak year is variable, as are the peak-year densities (Pearson 1966, Garsd and Howard 1981). We investigated the influence of variation in the frequency of occurrence of peak and crash years with a stochastic model

$$\mathbf{n}(t+1) = \mathbf{A}_t \mathbf{n}(t) \tag{9}$$

in which the projection matrix $\mathbf{A}_t$ was generated by a 3-state Markov Chain model of the environment (Figure 2). As in the periodic model, a peak year was always followed by a crash year and a crash year was always followed by at least one average year. There was a probability q that an average year was followed by a peak year and a probability $(1-q)$ that an average year was followed by another average year.

We varied the expected frequency of crash years, f, over the same range as in the periodic model, from once every three years to once every twelve years. The long-term frequency satisfies

$$f = \frac{2q+1}{q} \tag{10}$$

We investigated the same range of intensity of impairment as in the periodic model, independently reducing each demographic parameter by 0% to 50%. We estimated the stochastic population growth rate as the average growth rate of the population over 100,000 time steps (Caswell 2001). That is,

$$\log \lambda_s = \sum_{t=0}^{T-1} \log\left(\frac{N(t+1)}{N(t)}\right) \tag{11}$$

where $N(t) = \| \mathbf{n}(t) \| = \sum_i |n_i(t)|$ is the total population size and $T = 110,000$ is the length of the simulation. The first 10,000 time steps of the simulation were discarded to allow convergence to the stationary distribution and thus remove any transient effects.

We calculated the stochastic growth rate and the elasticity of the stochastic growth rate to changes in the parameters for each combination of frequency and intensity of impairment. The elasticity of $\log \lambda_s$ to change in a parameter θ was calculated as

$$\frac{\partial \log \lambda_s}{\partial \log \theta} = \frac{1}{T} \sum_{t=o}^{T-1} \frac{J_t \, \theta_t \, \mathbf{v}^T(t+1) \, \frac{\partial \mathbf{A}_t}{\partial \theta} \, \mathbf{w}(t)}{R(t) \, \mathbf{v}^T(t+1) \, \mathbf{w}(t+1)} \tag{12}$$

where

$$R(t) = \frac{\| \mathbf{A}_t \mathbf{w}(t) \|}{\| \mathbf{w}(t) \|} \tag{13}$$

(Caswell in press). Here, J_t is an indicator variable defining the type of year in which θ is perturbed. To calculate the elasticity of $\log\lambda_s$ to θ in all years $J_t = 1$. To calculate the elasticity of $\log\lambda_s$ to θ in crash years $J_t = 1$ if the environment is a crash year and 0 otherwise.

We calculated Monte Carlo standard error estimates for $\log\lambda_s$ in the same manner as for the periodic model, drawing parameters independently from gamma or beta distributions for reproduction and survival, respectively. Standard errors for $\log\lambda_s$ were calculated from 1,000 iterations.

RESULTS

Time-specific dynamics

The long-term population growth rates for constant conditions corresponding to average, peak or crash conditions varied widely, from 0.396 to 1.320 (Table 1). These growth rates are hypothetical projections since conditions do not remain in one of these states over time.

However, they show that Burrowing Owls are clearly capable of substantial population growth in peak years and may suffer substantial losses in crash years.

The stable stage and reproductive value distributions were fairly consistent among years. The stable stage distribution under peak year conditions was approximately a 66:33 ratio of juveniles to adults. In all other years the stable stage distribution was approximately a 50:50 ratio of juveniles and adults. The reproductive value of adults was about four times that of juveniles under all conditions.

The elasticities of λ to the parameters were similar in average and crash years (Fig. 3). The elasticities of λ to apparent juvenile survival and to fecundity were lower than to apparent adult survival in these years. The pattern of elasticities was reversed for peak year conditions. Under these conditions the elasticities of λ to apparent juvenile survival and fecundity were higher than to apparent adult survival. For the life cycle structure we used, which featured two stages with all possible transitions, the elasticities of λ to apparent juvenile survival and to fecundity are always equal in the time-invariant, deterministic case. Although the elasticities of λ to elements of the transition matrix always sum to unity, the elasticities of λ to parameters in the model do not. Transient dynamics did not appear to be important under constant conditions. Convergence to the stable stage distribution was reached in one or two time steps for matrices for all years.

The LTRE analysis indicated that the higher λ observed for peak year conditions was almost entirely a result of increased fecundity (Table 2). Both adult and juvenile apparent survival differed little between average and peak years, and made little contribution to the difference in λ under these conditions. The lower λ observed under crash conditions was mostly a result of reduced apparent adult survival (54%) and apparent juvenile survival (34%).

Deterministic periodic dynamics

For the periodic model, Burrowing Owl population growth rate increased as the frequency of vole peak-crash events declined and the intervening conditions predominated (Fig. 4). Confidence intervals for λ_{pd} were wide as a result of large standard errors for the parameters (Fig. 4). However, the increasing relationship between λ_{pd} and length of the vole cycle was observed in more than 90% of runs. This suggests the uncertainty in λ_{pd} may shift the line for the mean estimates up or down, but it would not change the relationship.

When cycle length was short, small alterations to the frequency of crash years had a greater effect on λ_{pd} than small parameter reductions (Figs. 5 and 6). Decreasing the frequency of vole peak-crash events from once every three years to once every four years resulted in a 3.3% increase in λ_{pd} (Figs. $4-6$). Fecundity in crash years would need to be reduced by nearly 50% to cause a change in λ_{pd} of an equivalent magnitude for a vole cycle of this length. However, the magnitude of the change in population growth diminished with increasing numbers of intervening years. These results are not dependent on the fact that estimates of reproduction and survival already incorporate impacts in crash years. The percentage change in λ_{pd} resulting from changes in the frequency or intensity of modeled impacts are similar if baseline parameter values in crash years are increased to equal those estimated for average years. Evaluating the effect of measured levels of p,p'DDE on population growth rate for the Lemoore Burrowing Owl population was not possible without more information on vole population dynamics in the region.

A reduction in adult or juvenile apparent survival had a greater effect on λ_{pd} than a reduction in fecundity (Figs. 5 and 7). The elasticities of λ_{pd} to s_a, s_j and b in crash years were low in the periodic model, even for short intervals between vole crash years (Fig. 7). The elasticities for these parameters all decreased as the interval between vole crash years increased, because this decreased the frequency at which they were perturbed. The similarity between the elasticities of λ_{pd} to apparent adult and juvenile survival were a consequence of the particular parameter values used in the model (see Table 1) and not a constraint of the periodic model structure. Different values for these parameters would not necessarily result in such similar elasticities.

There were negligible transient dynamics in the periodic model. The subdominant eigenvalue, $\lambda_{pd(2)}$, is nearly zero, so convergence is extremely rapid.

Stochastic dynamics

Results for the stochastic model were very similar to results for the periodic model. Population growth rate for the stochastic model, λ_s, was very similar to the periodic model, λ_{pd}, and the population growth rate confidence intervals for the two models were almost completely overlapping (Fig. 4). λ_s showed the same response as λ_{pd} to changes in cycle length and reductions in the three demographic parameters (Fig. 5). The elasticities of λ_s to the parameters and the change in the elasticities with cycle length were nearly identical in the stochastic and the periodic models. These results suggest that conclusions about population growth in a deterministic environment with variable vole densities are robust to the inclusion of stochasticity.

Discussion

Effects of frequency and intensity of contaminant impacts

Contaminant impacts on this Burrowing Owl population are mediated by the population dynamics of voles, their major prey species, because p,p'DDE effects are only observed when rodents are less frequent in the diet. We found a non-linear relationship between vole crash frequency and owl population growth rate. The impact of vole peak-crash events on Burrowing Owl population growth rate therefore depends on the frequency at which vole peak-crash events occur. Frequent vole peak and crash events result in substantial reductions in Burrowing Owl population growth rate. Long vole cycles, in which peak-crash events occur less than once every ten years, have a much smaller impact.

The relative importance of vole cycle length and of contaminant effects on parameters to Owl population dynamics also depends on the frequency of vole peak-crash events. A change in the frequency of vole peak-crash events from once every four years to once every three years decreased population growth rate by about 3.3%. Owl reproductive impairment in vole crash years would need to be nearly 50% to cause an equivalent decrease. However, as the interval between vole peak-crash events increased to ten years, a relatively small decline in owl productivity of 10% becomes equally important to owl dynamics as a one-year change in the vole cycle length. These general patterns appeared to be robust to the range of parameter values and the types of models we investigated.

The effect of vole peak-crash events on the Lemoore Burrowing Owl population depends on the frequency at which these events occur. Determining the relative importance of vole peak-crash events and reproductive impairment also requires estimates of reproductive impairment and of variability in both vole peak-crash events and reproductive impairment. Unfortunately we do not have data to estimate either the frequency or variability of vole peak-crash events. Vole populations at Lemoore peaked once between 1996 and 2001, or once in six years, but evidence exists for both more frequent and less frequent major fluctuations in vole populations in California. Evaluating more specific effects on the demography of Burrowing Owls at Lemoore will require a better understanding of vole population dynamics in the region.

Vole populations in California typically do not show the extremely regular patterns so prevalent at higher latitudes (Pearson 1966, Garsd and Howard 1981, Cockburn and Lidicker 1983). The driving factors of vole population dynamics are not well understood. Small rodents in Chile responded to the El Nino Southern Oscillation (ENSO) event in 1991 with greatly increased densities (Jaksic et al. 1997), and the vole population increase documented at Lemoore began in an ENSO year (1998). However, earlier records of increased vole abundance in California (Pearson 1966, Garsd and Howard 1981, Cockburn and Lidicker 1983) do not match up with ENSO events. Food does appear to be at least partially responsible for vole density increases, but many other factors are likely to be involved (Garsd and Howard 1981, Ford and Pitelka 1984). A major challenge to understanding how contaminant impacts are affected by other environmental conditions will be understanding how these conditions themselves are determined.

Greater population growth in Burrowing Owls in years when voles were abundant resulted primarily from increased reproduction. This is consistent with other studies that suggest that food availability is a major determinant of nesting success in Burrowing Owls (Wellicome 2000, Haley 2002). The potential for substantial population growth is no doubt driven partly by the large clutch size of this species (up to 12 eggs, Haug et al. 1993). Elasticity analyses also showed reproductive output was more important in peak than in crash vole years. Shifts such as this in the importance of different parameters under different conditions have seldom been documented with real data, but are beginning to be recognized and are no doubt more common in species in highly variable environments (Wisdom et al. 2000, Smith et al. in press). The life history characteristics required to generate such variable patterns are worth further exploration. Burrowing Owls may produce from none to over ten fledglings per nesting attempt, depending on annual conditions (Haug et al. 1993, Gervais and Anthony 2003). They appear to follow a strategy of maximizing reproductive output in years when conditions are favorable, but not investing greatly in reproduction in unfavorable years. This life history strategy, in conjunction with the variable environmental conditions, is likely responsible for the reversals in elasticity values.

The stochastic and periodic analyses demonstrated that apparent survival of both juvenile and adult owls was relatively more important than fecundity. These analyses represent an integration of the different annual conditions, and are therefore more reflective of reality than the hypothetical case where a single set of environmental conditions is projected over a long period of time. We had expected fecundity to be more important for the Burrowing Owl, a short-lived species capable of producing a large number of offspring (Emlen and Pikitch 1989, Heppell et al. 2000). The small impact of fecundity in our analyses was due in part to low reproductive output in average years. The importance of fecundity becomes greater as reproductive output increases.

Most previous studies investigating the effects of p,p'DDE on individuals found greater effects on reproduction than on survival at exposure levels comparable to those documented at Lemoore (Blus 1995, 1996, and references therein; Keith and Mitchell 1993). Because contaminant effects on reproduction in this study population occur when reproduction has relatively little impact on population-level processes, fairly severe contaminant effects on reproduction are necessary to substantially alter population growth. It is therefore not surprising that even high levels of reproductive impairment had relatively little effect on Burrowing Owl population dynamics in our models.

Burrowing Owl survival was likely severely underestimated in the vole crash years as a result of increased emigration following widespread reproductive failure (e.g. Jackson 1994, Wicklund 1996, Serrano et al. 2001, Catlin 2004). However, no estimates of emigration or immigration are available for this population. Estimation of fecundity is also known to be negatively biased (Gorman et al. 2003); therefore, no inferences should be made regarding absolute values of population growth rate, as they are clearly biased low. Movement in particular cannot be ignored if unbiased estimates of population growth or an indication of population status are desired.

The link between individual-level effects and population-level consequences lies at the heart of ecotoxicology (Truhaut 1977, Moriarty 1983, Caswell 1996, Stark and Banks 2000). Demographic models provide a powerful tool for making this link, especially for longer-lived organisms for which data are more difficult, time-consuming and expensive to collect. In many cases, experimental work will not be possible due to issues of scale and ethical constraints. Demographic models have many benefits. First, they provide a simple, flexible framework for evaluating population impacts. It is simple to incorporate different stressors on different life stages or at different points in the life cycle, to evaluate potential changes in environmental conditions, and to account for uncertainty in the data (e.g. by calculating confidence intervals). Second, demographic models synthesize the effects of toxicants into overall indices of population performance, such as population growth rate. Third, the lack of "complete" data is not an impediment to demographic modeling. Models can explore the potential impacts of unknown parameters and identify the most important pieces of missing information.

Our analyses show that demographic modeling can provide a reasonable analysis of contaminant effects at the population level even given uncertainty about the structure of the system and the owl's response to the environment. The Burrowing Owl is a fairly typical example of population-level risk assessment where only some demographic data are available. Although more complex models may be necessary to answer specific questions regarding risk or particular management strategies, our simple model captures the essential dynamics and is flexible enough to integrate effects occurring at varying temporal scales. Despite the wide confidence intervals in estimated population growth rate, the response of λ to changing vole cycle frequencies and demographic rates was consistent across a range of analyses that included both periodic and stochastic models. In this case, a simple model provides insight into the risk posed by an anthropogenic stressor and provides useful information for management and future research.

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Tables

Table 1: Estimates of adult survival (s_a), juvenile survival (s_j), fecundity (b), the number of nesting pairs (data from Gervais 2002), and population growth rate (λ) for time-invariant models for 1997 to 2000 .

Year	Adult survival (SE)		Juvenile survival (SE)		Fecundity (SE)		Number of pairs	λ
1997	0.540	(0.120)	0.277	(0.100)	1.175	(0.249)	65	0.866
1998	0.557	(0.071)	0.292	(0.056)	0.975	(0.168)	63	0.842
1999	0.575	(0.065)	0.307	(0.053)	2.426	(0.244)	85	1.320
2000	0.294	(0.053)	0.120	(0.025)	0.850	(0.198)	64	0.396

Table 2: Percent contribution of demographic parameters to the change in λ in peak (1999) and crash (2000) years relative to average (the mean of 1997 and 1998) years from an LTRE analysis.

			% contribution		
Year		change in λ	s_a	s_j	b
Peak	(1999)	0.454	0.058	0.087	0.880
Crash	(2000)	-0.470	0.542	0.337	0.097

Figure captions

Figure 1. Two-stage Burrowing Owl female life cycle based on a post-breeding census: s_a is adult survival, s_j is juvenile survival, and b is fecundity.

Figure 2. Transition graph for the 3-state Markov Chain for the stochastic model, Avg, Peak and Crash correspond to average, peak, and crash year conditions, respectively, and q is the probability of an average year being followed by a peak year.

Figure 3. The elasticity of population growth rate to apparent adult survival, s_a, apparent juvenile survival, s_j, and fecundity, b, for the time-invariant matrices $\mathbf{A}_{97}, \mathbf{A}_{98}, \mathbf{A}_p, \mathbf{A}_c$.

Figure 4. Population growth rate for the periodic model (λ_{pd}; heavy solid line) and stochastic model (λ_s; heavy dashed line) as a function of the interval between vole crash years. Light lines are ± one SE from bootstrap estimates of population growth rate.

Figure 5. Population growth rate for the periodic model (λ_{pd}; left panels) and stochastic model (λ_s; right panels) as a function of interval between vole crash years and percentage reduction in (a,b) apparent adult survival s_a, (c,d) apparent juvenile survival s_j, and (e,f) fecundity b. The white contour lines represent lines of equal population growth rate. The near vertical alignment of these contours demonstrates the small response of λ_{pd} and λ_s to parameter reductions. A greater change is seen along the x-axis, showing a greater response to changes in the frequency of vole crashes. Note the difference in scale on the y-axis for reductions in fecundity.

Figure 6. Percent change in λ_{pd} resulting from a 10% decrease in reproduction (dashed line) or from a one year increase in the number of average years occurring between vole peak-crash events (solid line).

Figure 7. Elasticity of population growth rated for the periodic model, λ_{pd}, to apparent adult survival (s_a), apparent juvenile survival (s_j) and fecundity (b) in vole crash years as a function of the interval between vole crash years. The elasticity of λ_{pd} to s_a and s_j for a given interval are identical.

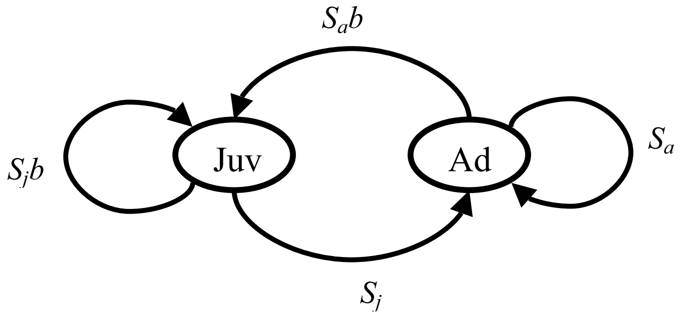

Figure 1:

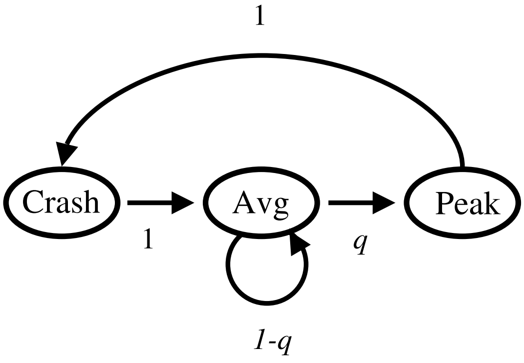

Figure 2:

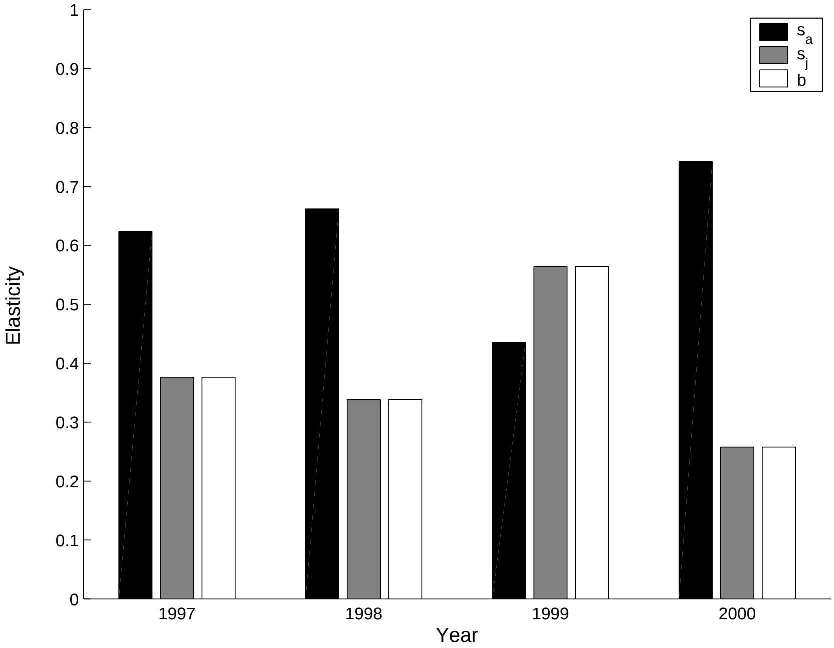
Elasticity
Year
1997
1998
1999
2000
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
s_a
s_j
b

Figure 3:

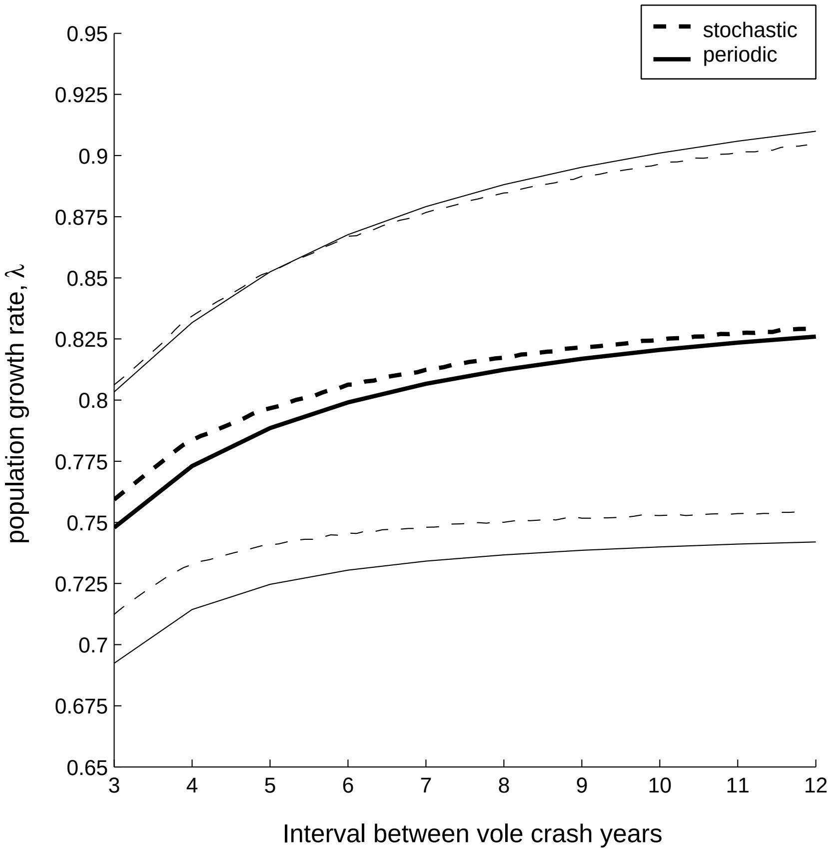
stochastic
periodic
population growth rate, λ
0.95
0.925
0.9
0.875
0.85
0.825
0.8
0.775
0.75
0.725
0.7
0.675
0.65
3
4
5
6
7
8
9
10
11
12
Interval between vole crash years

Figure 4:

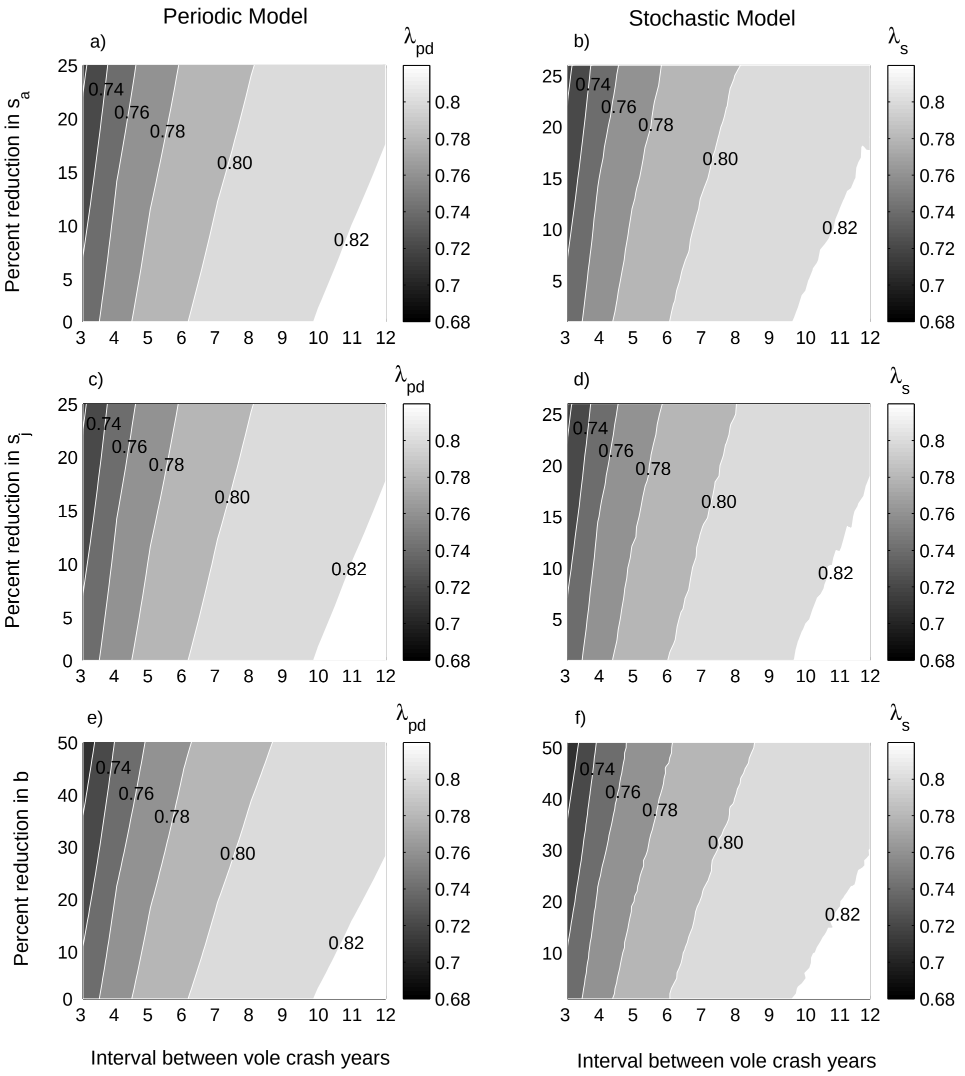
Periodic Model
Stochastic Model
a)
b)
c)
d)
e)
f)
λ_{pd}
λ_s
Percent reduction in s_a
Percent reduction in s_j
Percent reduction in b
Interval between vole crash years
0.74
0.76
0.78
0.80
0.82
0.8
0.78
0.76
0.74
0.72
0.7
0.68
3 4 5 6 7 8 9 10 11 12
0 5 10 15 20 25
0 10 20 30 40 50

Figure 5:

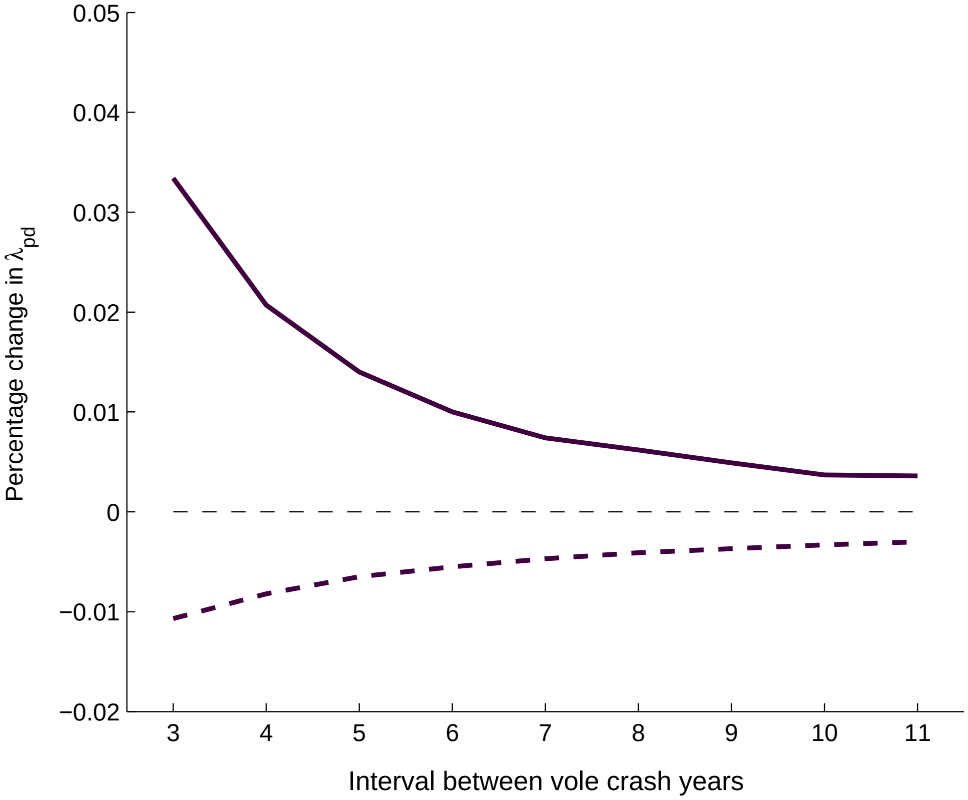
0.05
0.04
0.03
0.02
0.01
0
−0.01
−0.02
Percentage change in λ_{pd}
3
4
5
6
7
8
9
10
11
Interval between vole crash years

Figure 6:

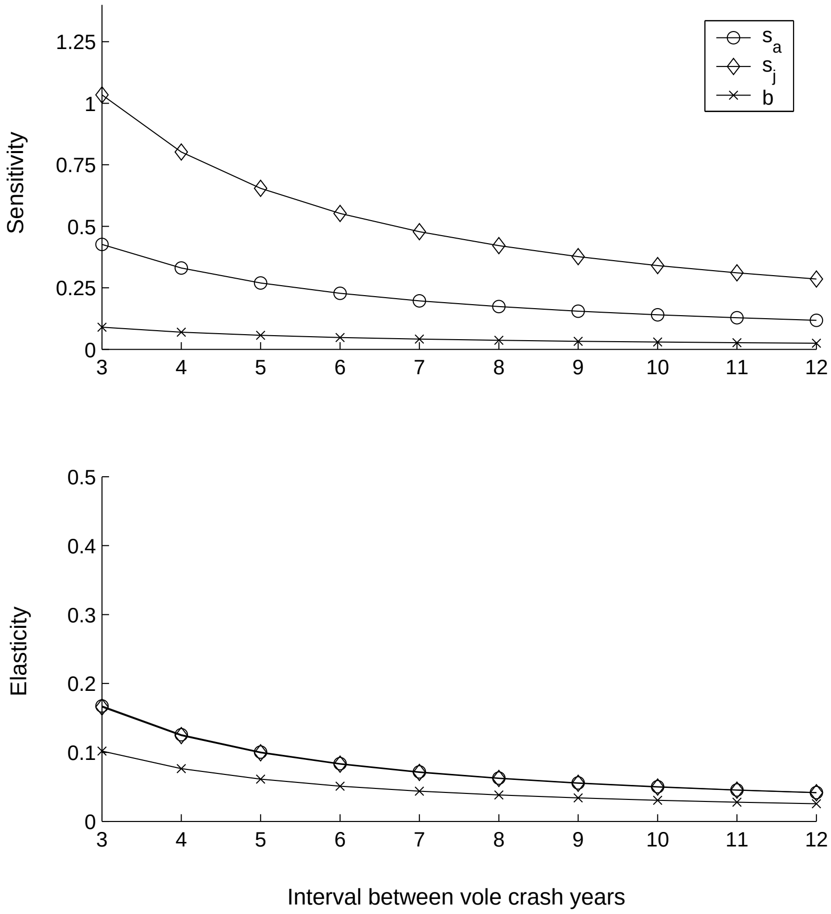
Sensitivity
1.25
1
0.75
0.5
0.25
0
3
4
5
6
7
8
9
10
11
12
s_a
s_j
b
Elasticity
0.5
0.4
0.3
0.2
0.1
0
3
4
5
6
7
8
9
10
11
12
Interval between vole crash years

Figure 7: