

# Short- and long-term population response to changes in vital rates: implications for population viability analysis

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**Abstract.** Conservation practitioners use demographic population viability analysis (PVA) to understand long-term effects of changing demographic rates on population growth rate. Sensitivities and elasticities of stage-specific survival and fertility rates provide managers with guidelines on the relative contributions of various life-history stages to long-term population growth. However, short-term patterns, especially single-year effects, of elasticity may be dramatically different from long-term effects, calling for caution in implementing management policies focusing entirely on only long- or short-term elasticities. Here we illustrate the temporal and spatial variation in elasticity patterns for four populations of California sea lions. Short-term stochastic elasticities were significantly different from long-term elasticities, and spatial patterns of short- and long-term elasticities varied across sites. These differences may be explained by transient effects in age structure and deviations from the stable age distribution, as well as environmental variation. Our results suggest that conservation practitioners should consider calculations of both short- and long-term elasticity in viability analyses that are used to guide management and should use caution in generalizing elasticity patterns across populations.

**Key words:** demography; elasticity; long-term; management; PVA; sea lion; short-term.

## INTRODUCTION

A major component of population viability analysis (PVA) is the analysis of stage-specific population models to quantify the relative contributions of vital rates (fertility, survival, and so on) to population growth rate (Morris and Doak 2002). In the absence of temporal variation, this can be done by calculating elasticities of the deterministic population growth rate given by the dominant eigenvalue of the population projection matrix (Caswell 2001). Recent studies (Boyce et al. 2006, Morris et al. 2008) have documented the long-term effects of environmental variation on stage-specific vital rates and the consequences for population viability in a variety of plant and animal species. In varying environments, elasticities of long-term stochastic growth rate (Tuljapurkar et al. 2003) determine the response of population growth to changes in vital rates. While demographic PVA helps in devising long-term management policies by quantifying the response of long-term population growth rate to changes in vital rates, they fail to address the effects of short-term changes in vital rates, including transient effects, on annual population growth rates. Recent work (Fox and Gurevitch 2000, Koons et al. 2005, Caswell 2007, Haridas and Tuljapurkar 2007) shows that transient effects can produce population responses that are very different than those predicted by

long-term measures. Temporal variation can further enhance the divergence between long and short-term elasticities.

Comparison of elasticities across sites has important conservation implications given that demographic data for many endangered species may be limited to a single site but management decisions must to be made for multiple populations. Furthermore, most viability analyses do not distinguish between long- and short-term effects in analyzing spatial patterns of elasticity, which may lead to erroneous conservation decisions. Morris and Doak (2005), in a comparative study of long-term elasticities for a population of a long-lived perennial plant moss campion (*Silene acaulis* L. [Caryophyllaceae]) sampled at five adjacent sites found that no single age-specific vital rate was most elastic across sites but mean survival rates combined for all ages had the highest elasticity. In this paper, we examine this issue more broadly for a long-lived vertebrate, California sea lions (*Zalophus californianus californianus*) by comparing short and long-term elasticities across four sites in the Gulf of California.

In particular, we address two issues in this paper: first, how do short-term elasticities for a population compare with long-term elasticities in a varying environment? We are especially interested in single-year effects wherein one examines change in annual population growth rate resulting from a change in a vital rate in a single year.

Second, how do elasticities, both long-term and short-term, vary across populations of the same species? We calculate two stochastic elasticities, elasticity with

Manuscript received 22 April 2009; accepted 9 June 2009; final version received 27 July 2009. Corresponding Editor: D. F. Parkhurst.

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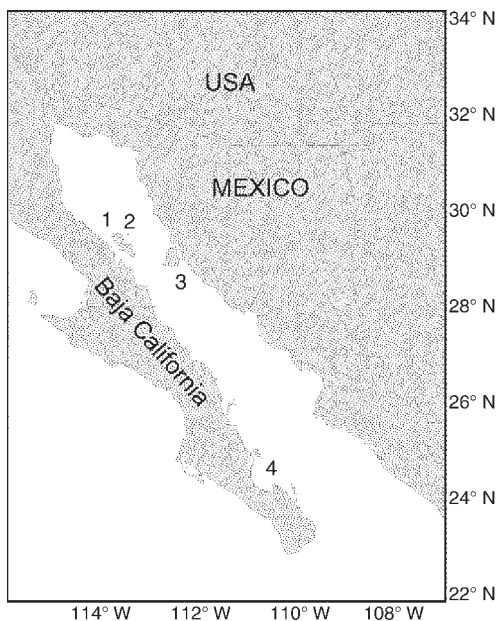


FIG. 1. Map of the Gulf of California, Mexico, highlighting the four islands where demographic data for sea lions were collected: (1) Granito, (2) Los Cantiles, (3) San Pedro Martir, and (4) Los Islotes.

respect to the mean of a vital rate and elasticity with respect to its variance (Tuljapurkar et al. 2003, Morris and Doak 2005), for four populations (Granito, Los Cantiles, San Pedro Martir, and Los Islotes; see Fig. 1) of California sea lions in the Gulf of California (GoC), Mexico. These populations have shown distinct demographic dynamics in terms of population growth, long-term extinction risks and age-specific demographic rates (Gonzalez-Suarez et al. 2006, Wielgus et al. 2008). Among the four populations, Los Islotes is increasing in abundance while Granito is declining and the remaining two seem to be nearly stable (Wielgus et al. 2008). There are limited data on movement among these populations and such data are generally difficult to obtain (Baguette et al. 2000).

Entanglement in fishing gear represents a significant threat to sea lion populations in the Gulf of California (Zavala-González and Mellink 1997, Auriolos-Gamboa et al. 2003, Underwood et al. 2008). Changes in climate, disease and poisoning are among other threats to sea lions in the Gulf (Heath 2002). Over the past three decades, the abundance of sea lions in the Gulf has declined by 20% (Szteren et al. 2006).

We compare variance elasticity across populations, which provide insight on how different populations might respond to increase in variance in demographic rates due to future climatic changes. We also analyze short-term effects of changing vital rates on annual growth rates by calculating short-term components of asymptotic elasticities. For each population we compare short and long-term elasticities and compare them

across populations to see how they generalize. We conclude with a discussion of how our results may be used to strengthen the application of demographic population viability analysis in conservation decision making.

#### DATA AND METHODS

We analyze demographic data collected between 1984 and 1998 for California sea lions from four islands (Granito, Los Cantiles, San Pedro Martir, and Los Islotes) in the GoC (Fig. 1). Population counts for each year are classified (Wielgus et al. 2008) as pups (0–1 yr), juveniles (1–4 yr), and adult females (>4 yr). A life-cycle diagram (Fig. 2) showing the three stages and annual transition between them helps in construction of the population model.

A  $3 \times 1$  population vector denoting counts in year  $t$  is given by  $\mathbf{P}(t)$  and  $\mathbf{A}$  denotes the projection matrix consisting of demographic rates (Fig. 2), explicitly given by

$$\mathbf{A} = \begin{pmatrix} 0 & 0 & F \\ G_p & S_j & 0 \\ 0 & G_j & S_a \end{pmatrix}.$$

Here  $F$  is the fertility rate per adult female,  $G_p$  is the fraction of pups that grow to juveniles in one year,  $S_j$  is the fraction of juveniles surviving and remaining in the juvenile stage (hereafter called juvenile stasis),  $G_j$  is the fraction of juveniles that grow to adults, and  $S_a$  is the adult survival rate. The parameters are estimated using quadratic programming (Wood 1997, Wielgus et al. 2008). To incorporate temporal variation we assume that survival rates  $G_p$ ,  $S_j$ , and  $G_j$  are time-dependent random variables with a beta distribution,  $B(a, b)$  with parameters  $a$  and  $b$ . These rates show more variation compared to  $F$  and  $S_a$  (Wielgus et al. 2008). Parameters of the beta distribution are determined by fixing their means as obtained from quadratic programming described above and by fixing the standard deviation at the observed level, reported in

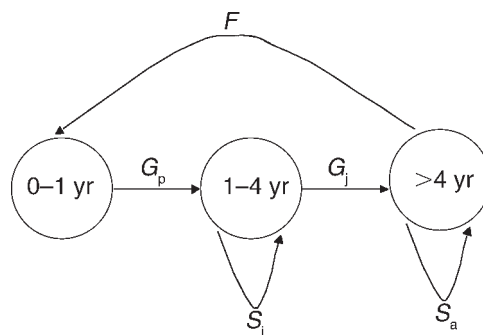


FIG. 2. Life cycle diagram for the life history of California sea lions used in the matrix model. The three life stages are pups (0–1 yr), juveniles (1–4 yr), and adult females (>4 yr) as classified in Wielgus et al. (2008). Arrows represent annual transition rates between the stages: fertility rate,  $F$ ; pup survival,  $G_p$ ; juvenile survival (and stasis),  $S_j$ ; juvenile survival,  $G_j$ ; and adult survival,  $S_a$ .

Wielgus et al. (2008). Distributions for survival for most populations are difficult to obtain due to lack of data. Choice of the beta distribution to model environmental variation has advantages since it can exhibit different shapes and is bounded between 0 and 1 (Morris and Doak 2002). The population model then can be written as

$$\mathbf{P}(t) = \mathbf{A}(t)\mathbf{P}(t - 1) \tag{1}$$

where  $\mathbf{A}(t)$  is now given by

$$\mathbf{A}(t) = \begin{pmatrix} 0 & 0 & F \\ G_p(t) & S_j(t) & 0 \\ 0 & G_j(t) & S_a \end{pmatrix}.$$

*Growth rates and elasticities*

We iterated the model (given by Eq. 1) 100 000 times and computed annual growth rates ( $\lambda_t$ ) as ratios of total sizes in adjacent years and the long-run stochastic growth  $\lambda_S$  (Caswell 2001) as

$$\log \lambda_S = (1/T) \sum_{t=1}^T \log \lambda_t. \tag{2}$$

We calculated two stochastic elasticities of  $\lambda_S$ , one with respect to the mean of a vital rate ( $E^\mu$ ) and the other with respect to its variance ( $E^\sigma$ ) using the method given in Tuljapurkar et al. (2003). Elasticity with respect to the mean of a rate (denoted by  $E^\mu$ ) is the proportional change in  $\lambda_S$  for a small proportional increase in the mean of that rate without changing its variance. Similarly elasticity with respect to the variance of a rate (denoted by  $E^\sigma$ ) is the proportional change in  $\lambda_S$  for a small proportional increase in the variance of that rate without changing its mean. We note here that, for a rate with no variation,  $E^\sigma = 0$ . We focus on  $E^\mu$  and  $E^\sigma$  since they unambiguously represent the effects of changing means and variances on vital rates (Haridas and Tuljapurkar 2005). The net effect of variability on all stages of a population is given by the summary elasticity  $T^\sigma$ , which is the sum of variance elasticities ( $E^\sigma$ ) for all rates. Similarly the sum of mean elasticities ( $E^\mu$ ) for all rates is given by  $T^\mu$  and there is a constraint between  $T^\sigma$  and  $T^\mu$  given by  $T^\mu + T^\sigma = 1$ , which provides a tool to classify populations according to their response to environmental variation. In general, it has been observed (Pfister 1998, Morris et al. 2008) that, for long-lived species vital rates with more variation have less influence on population growth rate. Similarly short lived species are more prone to increases in temporal variation increasing their chances of extinction.

While the above elasticities describe the response of asymptotic long-term growth rate to changes in mean or variance of a vital rate, they may not be good indicators of short-term effects of changing vital rates on population growth rate (Gurevitch and Fox 2000, Caswell 2007, Haridas and Tuljapurkar 2007). The main reason for this is that a population is always likely to be away from the stable age distribution (SAD) and it

TABLE 1. Stochastic growth rate and total mean and variance elasticities for four populations of California sea lions (*Zalophus californianus*) in the Gulf of California.

Island	Stochastic growth rate $\lambda_S$	Total mean elasticity $T^\mu$	Total variance elasticity $T^\sigma$
LI	1.05	1.0042	-0.0042
LC	0.955	1.0114	-0.0114
GR	0.902	1.0231	-0.0231
SM	0.964	1.0088	-0.0088

Note: LI stands for Los Islotes, LC for Los Cantiles, GR for Granito, and SM for San Pedro Martir.

is especially possible that populations that face risk of extinction are not at their stable age distributions. Short-term elasticities describe the effects of changing a vital rate (or its mean/variance) on the population growth rate, assuming that the age-structure is fixed at the observed value in the beginning of the year (Coulson et al. 2004, Haridas and Tuljapurkar 2007). This measure is essentially a single-year effect and ignores effects due to changes in age structure, which happen in the long run, and could be different from the asymptotic elasticity depending upon the species life history. In deterministic environments, it was shown (Haridas and Tuljapurkar 2007) that long-term elasticity  $e_{ij}$  (of a vital rate denoted by matrix element  $(i, j)$ ) can be decomposed into two components  $e_{ij}^1$  and  $e_{ij}^2$ , where  $e_{ij}^1$  denotes the short-term single-year component due to changes in vital rates alone and  $e_{ij}^2$  denotes the long-term component due to changing age-structure. A similar decomposition holds in varying environments for stochastic elasticities (see Appendix for details) and in this paper we focus on the calculation of the component  $e_{ij}^1$  in a stochastic environment for  $E^\mu$  and  $E^\sigma$  and compare that with long-term elasticities of  $\lambda_S$ .

RESULTS

*Stochastic growth rate ( $\lambda_S$ ) and mean ( $E^\mu$ ) and variance ( $E^\sigma$ ) elasticities*

The stochastic growth rate  $\lambda_S$  is highest for Los Islotes and is lowest for Granito (Table 1). Using the constraint on summary elasticities  $T^\mu$  and  $T^\sigma$  given by  $T^\mu + T^\sigma = 1$ , we find that among the four populations, Granito is most responsive to temporal variation whereas Los Islotes is least affected by variation (Table 1). We also found that the stochastic growth rates  $\lambda_S$  decrease as the magnitude of  $T^\sigma$  increase. Long-term mean elasticities  $E^\mu$  for all vital rates are positive because an increase in the means of these rates leads to an increase in the population growth rate. Among all vital rates, the mean elasticity  $E^\mu$  is largest for adult survival ( $S_a$ ) for all populations (triangles in Fig. 3). Variance elasticities  $E^\sigma$  are negative for all vital rates, indicating that increasing variation in these rates reduces long-term growth rate. Variance elasticity is the highest for juvenile survival  $G_j$  for all populations, but note that in general these effects are small in magnitude for all rates (triangles in Fig. 4).

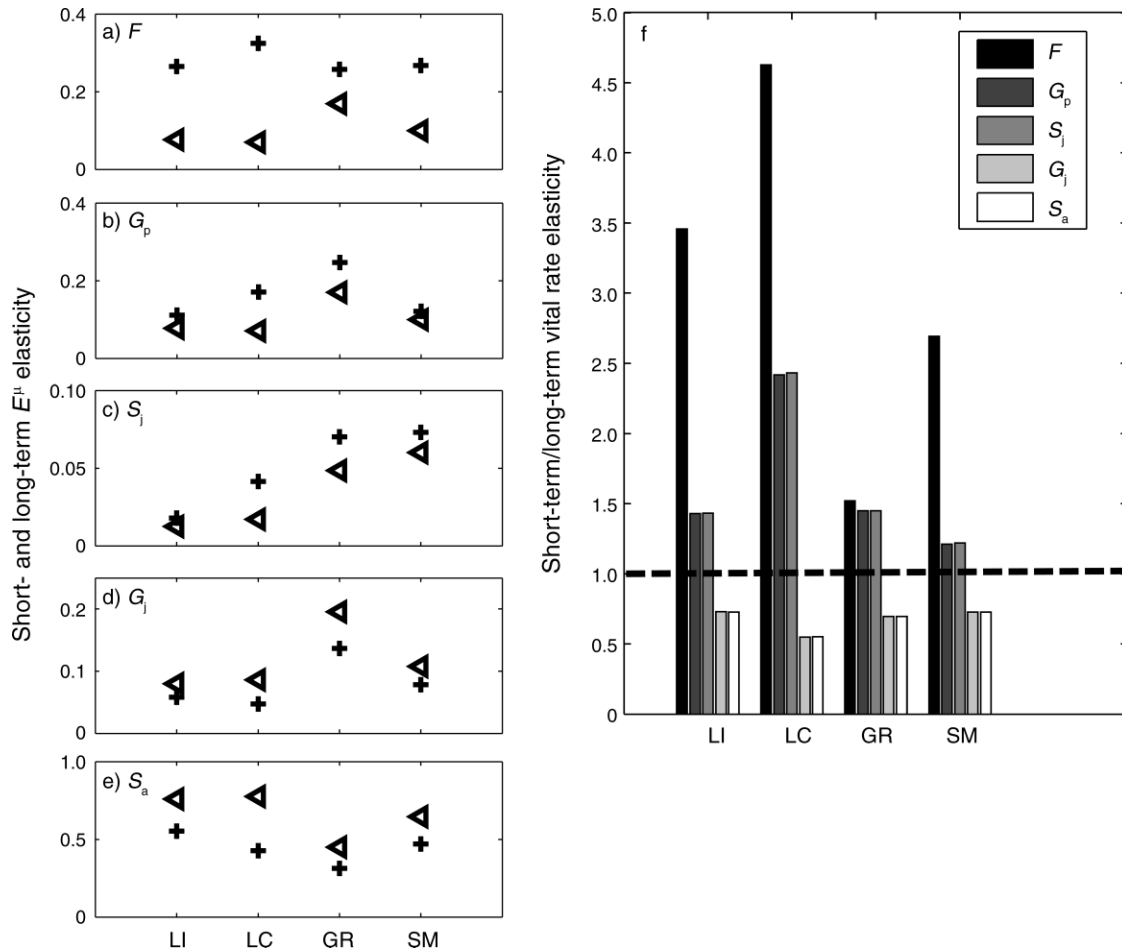


FIG. 3. Long-term  $E^H$  elasticities (triangles) and their short-term components (crosses) for (a) fertility rate,  $F$ ; (b) pup survival,  $G_p$ ; (c) juvenile stasis,  $S_j$ ; (d) juvenile survival,  $G_j$ ; and (e) adult survival,  $S_a$ . (f) Ratio of short-term over long-term elasticities of vital rates; the dashed line at 1 indicates when short- and long-term elasticities are equal in magnitude. Island names are as in Fig. 1.

#### Comparing short- and long-term elasticities

Short-term elasticity predicts the immediate change in annual growth rate when a vital rate (or its mean/variance) is changed without accounting for a corresponding change in age structure. We calculated short-term elasticities corresponding to changes in means of vital rates and compared that with long-term  $E^H$  values (Fig. 3). For all rates, short-term elasticities (denoted by stars) are different from their long-term effects (denoted by triangles). For fertility  $F$ , pup survival  $G_p$ , and juvenile stasis  $S_j$ , short-term elasticities are always larger than long-term mean elasticities whereas for juvenile survival  $G_j$  and adult survival  $S_a$  the pattern is reversed. While adult survival  $S_a$  has the largest long-term  $E^H$  elasticity (among all vital rates) for all populations (about 43% in Granito to 76% in Los Cantiles), it should be noted that short term elasticities for  $S_a$  are much smaller (about 31% in Granito to 55% in Los Islotes). For the fertility rate  $F$ , long-term  $E^H$  elasticities range from 7% (Los Cantiles) to 16% (Granito), whereas corresponding short-term elasticities are above 25% for

all populations (Fig. 3a). Examining ratios of long- and short-term  $E^H$  elasticities reveal the wide range of variation between populations (Fig. 3f). For instance, short-term elasticity of fertility  $F$  is about five times larger than corresponding long-term effect in Los Cantiles whereas in Granito short-term effect is only about 1.5 times that of long-term effect.

The general pattern emerging from above analysis shows that short term effects are more pronounced for vital rates corresponding to younger ages, including fertility, while long-term affects are higher for vital rates of older ages. Although variance effects are small in magnitude there are differences in short and longer-term effects. For pup survival  $G_p$  and juvenile stasis  $S_j$ , short-term variance elasticities are larger in magnitude while for juvenile survival  $G_j$  long-term effects are more pronounced than short-term effects (Fig. 4).

#### DISCUSSION

Demographic PVA models typically include estimates of long-term population growth rate and their determi-

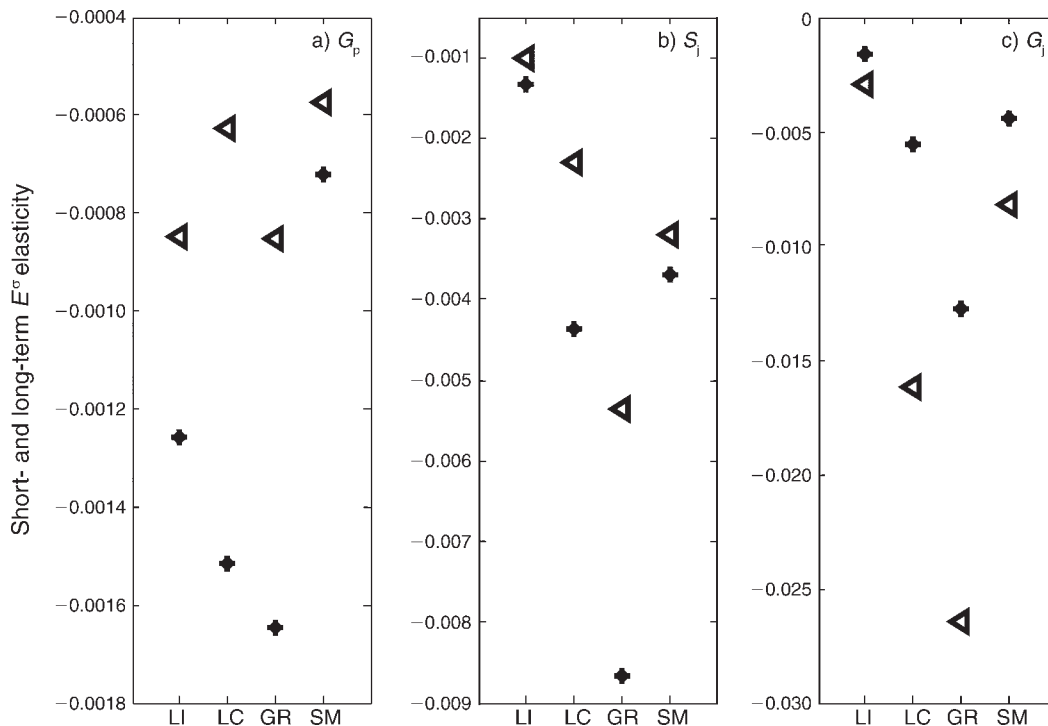


FIG. 4. Long-term  $E^\sigma$  elasticities (triangles) and their short-term components (crosses) for (a) pup survival,  $G_p$ ; (b) juvenile stasis,  $S_j$ ; and (c) juvenile survival,  $G_j$ .

nants in terms of sensitivities and elasticities (Morris and Doak 2002). In light of the impacts of transient and stochastic fluctuations, which may cause a population to deviate from its stable age distribution for long time periods, recent work (Fox and Gurevitch 2000, Koons et al. 2005, Caswell 2007, Haridas and Tuljapurkar 2007) has examined the importance of considering short-term effects. It is reasonable to assume that all populations and especially those facing risks of extinction often have skewed age-structures and respond differently to changing vital rates than when near their equilibrium age-structures. Vital rates that are important in the long-term may deviate from short term patterns, necessitating a closer analysis of both short- and long term measures of management. In this paper, we show that short- and long-term stochastic elasticities exhibit different patterns across four populations of California sea lions. While adult survival is generally the most elastic vital rate (Wielgus et al. 2008), we show that this may not be the case for shorter time periods, especially in single years. In fact, all rates exhibit considerable differences in short- and long-term elasticities, highlighting the importance of exercising caution in generalizing these effects across populations. For long-lived species like California sea lions, adult survival has been known to be more elastic than fertility (Pfister 1998, Gaillard et al 2000, Morris and Doak 2004), but this will depend upon initial age-structure and stochastic fluctuations. Our results show that fertility rate has considerable single-year effect on population growth suggesting that management efforts

should also focus on factors contributing to increased fertility. An improved understanding of mating behavior and demographic information pertaining to both sexes may help in devising helpful management strategies.

We note that in our model all individuals older than four years are included in the adult group (Wielgus et al. 2008), so the fraction of adults dominates the age distribution resulting in higher elasticity for adult survival. Ignoring management implications of the high short-term elasticity of fertility will skew age structure by reducing fraction of pups for longer time periods and will eventually result in the decline of long-term population growth rate.

We also show that in general, vital rates corresponding to younger ages, like pup survival as well as fertility, exhibit more short-term effects than rates corresponding to older ages like adult survival. This pattern, which holds across populations, will be especially pronounced for populations consisting of fewer younger individuals (than compared to the stable age distribution) that reduces the supply of individuals to adult reproductive age groups. This pattern also seems to be a general feature of all long-lived species where fertility and young survival will enhance population growth in years when the population is away from SAD while adult survival becomes prominent as the population grows to demographic stability.

We suggest that managers who employ demographic PVA methods consider calculations for both short and long-term elasticities before making policy decisions.

Long-term measures *assume* that a population has reached its equilibrium but that may not be true in many cases. Short-term effects can be revealed by analyzing single-year effects, by calculating annual growth rates and their elasticities. Such analyses use only observed annual data, computations are straightforward and we have provided necessary MATLAB codes in the online Appendix. Short term effects will be particularly apparent when demographic damping is slow and environmental disturbance skew age structure towards particular age groups. In the case of sea lions studied here, short-term policies should focus on strategies enhancing pup survival and fertility in all populations until populations reach demographic stability after which long-term policies may focus on adult survival.

## ACKNOWLEDGMENTS

This study was supported by a grant to L. R. Gerber from the National Science Foundation (Animal Behavior, Biological Oceanography, and International Programs; Award #0347960). We are grateful to SEMARNAT (Instituto Nacional de Ecología y Dirección de Administración de Pesquerías) for research permits (most recent, Oficio num/SGPA/DGVS/03269).

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## APPENDIX

Calculation of short-term elasticity (*Ecological Archives* A020-025-A1).

## SUPPLEMENT

Matlab code for calculating short-term elasticities for California sea lions (*Ecological Archives* A020-025-S1).