Journal of Applied Ecology

Journal of Applied Ecology 2014, **51,** 270–278 doi: 10.1111/1365-2664.12177

Two-sex matrix models in assessing population viability: when do male dynamics matter?

Leah R. Gerber* and Easton R. White

Ecology, Evolution and Environmental Science, School of Life Sciences, Arizona State University, Tempe, AZ 85287-4601, USA

Summary

1. While most demographic population models used in conservation rely on female vital rates, recent empirical evidence suggests that male dynamics should be included in population models used for assessing extinction risk.

2. Using California sea lions *Zalophus californianus* as an applied example, we demonstrate that there are situations in which two-sex models are more appropriate than the commonly used female-based model.

3. Two-sex models are relevant in cases where vital rates for sexes differ and for polygamous species such as sea lions. Vital rates targeted for management may therefore respond differently for males and females and for different assumptions about sex ratio.

4. *Synthesis and applications*. Conservation biologists should carefully consider the social structure and sex ratio of focal species in order to determine whether a two-sex matrix model will yield more accurate estimates of extinction risk than standard one-sex models.

Key-words: extinction risk, sex ratio, two-sex models, *Zalophus californianus*

Introduction

Population viability analysis (PVA) represents one of the most important developments in the field of conservation biology (Morris & Doak 2002). Most demographic population models make the simplifying assumption that populations can be represented based on female vital rates and male dynamics need not be included in these models (Caswell 2001). As a result, sex-specific vital rates are rarely incorporated into PVA (but see Ray, Gilpin & Smith 1991; Anthony & Blumstein 2000; Gerber 2006) or are included in complex individual-based models that require detailed behavioural information (e.g. Sutherland & Norris 2002; Le Galliard *et al.* 2005). At the same time, the behavioural ecology literature has begun to consider the role of mating systems in population dynamics (e.g. Le Galliard *et al.* 2005), but this work is generally not applied to conservation and management. Integration of insights from behavioural ecology with demographic population models may improve our ability to estimate risk of extinction. In this paper, we examine the importance of including both males and females in matrix population models to improve our understanding of extinction risk, using California sea lions as a case study.

For female-biased sex ratios, male limitation can occur when males are unable to access all females in breeding colonies, leading to a reduction in male fertility. Conversely, a male-biased sex ratio will reduce male fertility because there are fewer females and aggression increases at high male density. In cases of extreme bias in sex ratio and small population size, the number of males in a population generally increases female reproductive success. For example, dramatic declines in the abundance of the harem-building ungulate *Saiga tatarica tatarica* occurred due to an extremely low proportion of males in the population (Milner-Gulland *et al.* 2003). Here, the low relative abundance of males in the population led to reproductive collapse because dominant females prevented young females from breeding with rare males. Similarly, Le Galliard *et al.* (2005) found in common lizards *Lacerta vivipara* that an excess of adult males begets aggression towards adult females, leading to a decline in survival, fecundity and emigration. This suggests that extinction risk may be significantly influenced by both male and female population dynamics.

Male and female mortality appear to exhibit different dynamics for a wide range of taxa. In humans and many other mammals, mortality rates are higher for males, whereas in many birds female mortality is higher (Promislow 1991; Austad 2011). Mortality patterns also depend on age structure. In the Mediterranean fruit fly *Ceratitis*

---

*Correspondence author. E-mail: Leah.Gerber@asu.edu

capitata, female mortality is higher than male mortality in early ages, while this pattern reverses for older ages (Carey, Liedo & Vaupel 1995). Adult sex ratio and mating system produce variation in male and female reproductive success as in the case of red deer (Clutton-Brock, Guinness & Albon 1982). Sex-specific differences in life span, age at maturity and other demographic parameters have also been documented in many species of animals and plants (Meagher & Antonovics 1982; Delph 1999; Eppley 2001; Rankin & Kokko 2007; Barrett & Hough 2013). For instance, Bell (1980) found that males are about 40% older than females at maturity in many mammals and birds. Thus, male and female dynamics may differ, and a proper understanding of such population dynamics may necessitate the inclusion of both sexes in population models. Indeed, sexual dimorphism in vital rates may produce distinctly different dynamics from those predicted by one-sex models.

When vital rates are density-independent, one-sex matrix models are well understood. With data on age-specific survival and fertility rates, a one-sex matrix model is thought to accurately describe population dynamics. Here, population growth is exponential and the population approaches a stable age structure, such that the dominant eigenvalue (λ) of the matrix describes population growth. Measures that are useful in conservation and management include estimates of population growth, as well as short- and long-term sensitivities of population growth rate (Caswell 2001; Morris & Doak 2002). This is well developed for density-independent models (Caswell 2001), but little attention has been given to understanding such metrics in two-sex models (except see Shelton 2010 for a sensitivity analysis using a two-sex matrix model for two seagrass species to examine female-biased sex ratios). Two-sex models have been used for several species since the late 1990s; however, none compare one-sex with two-sex models, and none derive sensitivities for frequency-dependent models. The widely used software RAMAS (Applied Biomathematics, Setauket, NY, USA, 2007) has a module for including sex structure. One can choose options to model only females or males, and the model allows the user to select the mating system from monogamous, polygynous and polyandrous. There are several applications of this model in the published literature (e.g. Akcakaya *et al.* 2004a,b, 2005; Harveson *et al.* 2004; Bretagnolle & Inchausti 2005; Wintle *et al.* 2005; Hamel *et al.* 2006; Beaudry, deMaynandier & Hunter 2008; Guichón & Doncaster 2008; Robinson *et al.* 2008).

In conservation, we seek to develop the simplest model possible that allows for accurate assessments of population viability. Simple models that do not require extensive parameterization are practical for conservation practitioners (Ludwig & Walters 1985; Beissinger & Westphal 1998). At the same time, the development of matrix models that include the dynamics of both sexes could enhance the use of existing behavioural data in conservation biology (Rankin & Kokko 2007). In this paper, we evaluate the effects of ignoring males when estimating risk of extinction, using California sea lions as a case study. The Gulf of California (GoC) population of California sea lions include 13 island breeding colonies, each exhibiting distinct population trends. Our analyses rely on data collected at Los Islotes island, which is a small but increasing population of sea lions. Gulf of California sea lions are considered to be a population of conservation concern by the Mexican government (Szteren, Aurioles & Gerber 2006; Ward *et al.* 2009).

Materials and methods

ONE-SEX AND TWO-SEX MODELS FOR CALIFORNIA SEA LIONS

To compare one- and two-sex matrix population models, we consider four simple scenarios: one model includes vital rates for females only, and three models include vital rates for both males and females, but differ in how their fertility functions are modelled.

A female-based model for California sea lions (Wielgus *et al.* 2008) can be described by the equation,

$$\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t) \qquad \text{eqn 1}$$

where t is a time step of 1 year and the matrix A is given by

$$\mathbf{A} = \begin{pmatrix} 0 & 0 & F \\ Gp & Sj & 0 \\ 0 & Gj & Sa \end{pmatrix} \qquad \text{eqn 2}$$

The life stages are classified as pups (0–1 years), juveniles (1–4 years) and adult females (>4 years). Here, F is the fertility rate per adult female (number of offspring per female that survive through their first year), G_p is the fraction of pups that survive their first year, S_j is the fraction of juveniles surviving and remaining in the juvenile stage, G_j is the fraction of juveniles that grow to adults and survive, and S_a is the adult survival rate (Wielgus *et al.* 2008).

A two-sex model in which fecundity depends upon male and female abundances (Caswell & Weeks 1986; Lindström & Kokko 1998) is developed for California sea lions,

$$n(t+1) = \begin{pmatrix} 0 & 0 & \rho F_m & 0 & 0 & \rho F_f \\ Gp_m & Sj_m & 0 & 0 & 0 & 0 \\ 0 & Gj_m & Sa_m & 0 & 0 & 0 \\ 0 & 0 & (1-\rho)F_m & 0 & 0 & (1-\rho)F_f \\ 0 & 0 & 0 & Gp_m & Sj_f & 0 \\ 0 & 0 & 0 & 0 & Gj_f & Sa_f \end{pmatrix} \begin{pmatrix} P_m \\ J_m \\ A_m \\ P_f \\ J_f \\ A_f \end{pmatrix} (t) \qquad \text{eqn 3}$$

where P, J and A represent population size, at time t, for pups, juveniles and adults, respectively, and the subscripts m and f represent male and female classes. Female and male per capita fertilities are given by F_f and F_m, respectively, and ρ is the primary sex ratio (fraction of males at birth). The parameters Gp, S_j and S_a are now specified for males and females, denoted by subscripts m and f, respectively. Thus, in addition to a standard female-only matrix model, we consider three two-sex models reflecting alternative fertility functions.

We first assume that fertility is a scalar value as in the one-sex model. When other parameters are equal, this model reduces to the one-sex version (Equation 2). We then test two models where fertility is affected by both male and female abundance, using a harmonic fertility function (HFF) or a modified version (MHFF). These functions have been shown to be effective for two-sex matrix models (Legendre 2004; Miller & Inouye 2011). The HFF is described by Caswell (2001) as,

$$F_f = \frac{K \times N_m}{N_m + (N_f/h)} \qquad \text{eqn 4}$$

where N_m is the number of adult males, N_f is the number of adult females, h is the harem size, and K is the number of offspring per adult female, with a similar expression for male fertility. The modified HFF represents an extension of the HFF and assumes that the maximum number of pups a male–female pair can produce is one; thus, a particular female can only contribute half of a pup. Males are known to mate with groups of females (Flatz *et al.* 2012); thus, an individual male can actually produce more than half of a pup. Specifically, a male's reproductive output is limited by the number of females that can reproduce in a given year ($0{\cdot}5N_f$),

$$F_f = \min\left(0.5, \frac{K \times N_m}{N_m + (N_f/h)}\right) \qquad \text{eqn 5}$$

$$F_m = \min\left(\frac{0.5N_f}{N_m}, \frac{K \times N_f}{N_m + (N_f/h)}\right) \qquad \text{eqn 6}$$

The HFF and the MHFF are frequency-dependent (Caswell 2008). When $h = 1$, births are maximized when males and females are equally abundant. If $h > 1$, births are maximized when female abundance exceeds male abundance. In the general case of HFFs, increasing h makes the model much more dependent on female abundance (Caswell 2001); however, this is not always the case when considering the MHFF.

We parameterize our models with values calculated in past studies that utilized the 1978–2008 California Sea lion data set at Los Islotes in the Gulf of California (Table 1; Wielgus *et al.* 2008). We then initiate our simulations at the 1978 abundance level and run the model for thirty years. Although quadratic programming techniques indicate an adult survival rate of 0·950 at our study site (Wielgus *et al.* 2008), we also consider more general cases when adult survival rate varies.

EQUILIBRIUM AGE STRUCTURE AND POPULATION GROWTH RATE (λ)

Equilibrium age structure describes the age distribution of organisms when the population is at a stable age distribution (SAD). To illustrate the extent to which changes in vital rates may affect SAD in two-sex models, we examined the age distribution for California sea lions for a range of sex-specific survival rates. Here, when survival rates for males and females are equal, the equilibrium age structure includes an equal number for each sex (Fig. 1). Note that here we are examining the two-sex model with the modified HFF. A population at a SAD grows at a constant annual rate, described by the discrete rate of annual increase (λ). Although our two-sex model is frequency-dependent, it has a SAD and grows exponentially determined by the largest eigenvalue (λ) of the equilibrium projection matrix (Table 2). We also examined the sensitivity of λ by running our two-sex model with different combinations of male and female survival rates ranging from 0·1 to 1 (Fig. 3). Specifically, we held either male or female survival rate constant at 0·95 and varied the other sex's survival rate to determine the effect on λ. We also examined the effect of varying both sex's survival rate at the same time (Fig. 3).

ELASTICITY ANALYSIS

Elasticity analysis is an important tool in demographic PVA, allowing the identification of the life stages that contribute most to population growth so that management can focus on these stages (Caswell 2001). A linear analysis of elasticities is easily done using standard approaches in demography (Caswell 2001), whereas elasticity analysis in two-sex models has only recently been applied to conservation (Caswell 2008). We compare survival and fertility elasticities between the one- and two-sex models (Table 2). We calculated elasticities by producing elasticity matrices for each of our four models' transition matrices (see Caswell 2001). To evaluate the extent to which mating system affects population response to vital rates, we also evaluate the effect of various levels of polygyny on population growth rate by manipulating the harem size (h) (Fig. 2).

ESTIMATES OF EXTINCTION RISK

For threatened species, estimates of extinction risk provide important information for devising strategies for conservation and management. To compare extinction risk estimates for one- and two-sex models, we use a stochastic analogue of the models in Equations (2) and (3). We assume that all of our growth and survival parameters can be estimated as beta variables (Chirakkal & Gerber 2010). The beta distribution is an appropriate representation of environmental variation because the distribution can exhibit different shapes and is bounded between 0 and 1 (Morris

Table 1. Parameter definitions and values used in all four models described. In the two-sex models, all parameters are assumed to be equal for both sexes

Parameters	Meaning	Value	Source
K	Average litter size	0·912	Wielgus *et al.* (2008)
ρ	Primary sex ratio	0·5	Hernández-Camacho *et al.* (2008)
G_p	Fraction of pups that grow to juvenile stage class	0·437	Wielgus *et al.* (2008)
S_j	Fraction of surviving juveniles that remain in same stage class	0·147	Wielgus *et al.* (2008)
G_j	Fraction of juveniles that grow to adult stage class	0·478	Wielgus *et al.* (2008)
S_a	Adult survival rate	0·950	Wielgus *et al.* (2008)
h	Harem size per male	4·2	Young, Gonzalez-Suarez & Gerber (2008); Gerber (2006)

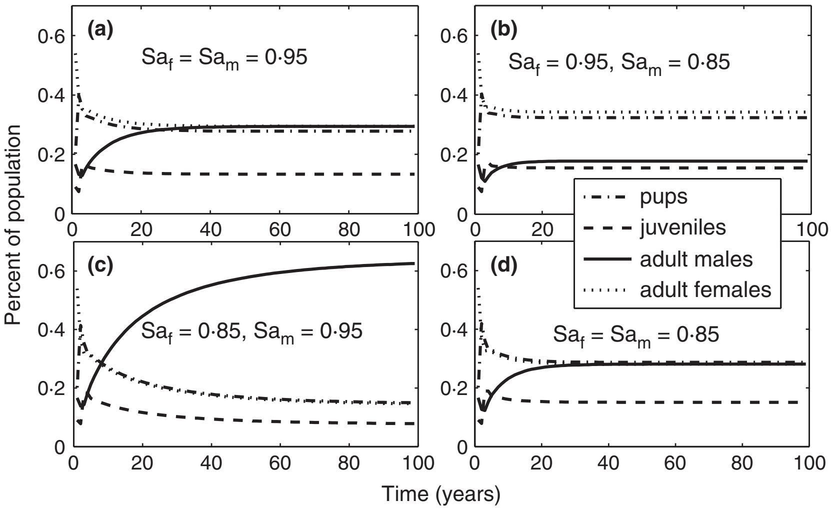

Fig. 1. Predicted age distribution [from model using the modified harmonic fertility function (HFF)] for California sea lions at Los Islotes island in the Gulf of California, with primary sex ratio $\rho = 0{\cdot}5$ and average harem size $h = 4{\cdot}2$. The initial cohort contains about 50% females. Survival rates for females (Sa_f) and males (Sa_m) are: (a) $Sa_f = Sa_m = 0{\cdot}95$; (b) $Sa_f = 0{\cdot}95$, $Sa_m = 0{\cdot}85$; (c) $Sa_f = 0{\cdot}85$, $Sa_m = 0{\cdot}95$; and (d) $Sa_f = Sa_m = 0{\cdot}85$.

Table 2. Elasticities of fertility and survival parameters for males and females in one-sex and two-sex models

	E_{F}	E_{Sa_m}	E_{Sa_F}	λ
One-sex	0·0792	NA	0·7495	1·050
Two-sex	0·0792	0·3738	0·3748	1·050
Two-sex (MHFF)	0·0836	0·3675	0·3675	1·058
Two-sex (HFF)	0·1045	0·3382	0·3321	1·098

The dominant eigenvalue (λ) of the transition matrix describes the discrete rate of population increase. MHFF is the two-sex model when using the modified fertility function, whereas HFF represents the standard harmonic fertility function (see Materials and methods).

& Doak 2002). Parameters of the beta distribution (α, β) are determined with method of moments estimators, which utilize the sample mean, and variance of each parameter in our model (Bain & Engelhardt 1991; Owen 2008). To calculate the appropriate beta distribution (i.e. specific shape parameters α and β), we used the mean and standard error for each parameter estimated by Wielgus *et al.* (2008). Simulated estimates of abundance, with stochastic growth and survival, are then used to estimate extinction risks from each of our four models. We ran the stochastic analogue of each model 1000 times and created distributions of the end population size after 30 years (Fig. 4).

MODEL EVALUATION

We compare the results from stochastic analogues of our four deterministic models (as described in the section *Estimates of Extinction Risk*) to six measurements taken in the field (population growth rate, end population size and stage distribution of pups, juveniles, adult males and adult females, Table 3). In order to accomplish this, we first calculated the population growth rate for 1000 simulations for each model to estimate a distribution of population growth rates. We use this distribution as a basis for comparison to our independent empirical estimate of population growth rate. We assess the model fit based upon when a field measurement falls within the 95% ($^{+}/_{-}$ 1·96σ) confidence interval of the corresponding measurement in a model simulation (Table 3). A similar procedure was used to generate distributions of end population size (year 30 of a simulation) for our models to compare to 2008 field data (30 years from the initial census in 1978). The stage distribution of each stage class was calculated as the proportion of individuals in a given stage divided by the total population size. We recorded the mean stage distribution for each

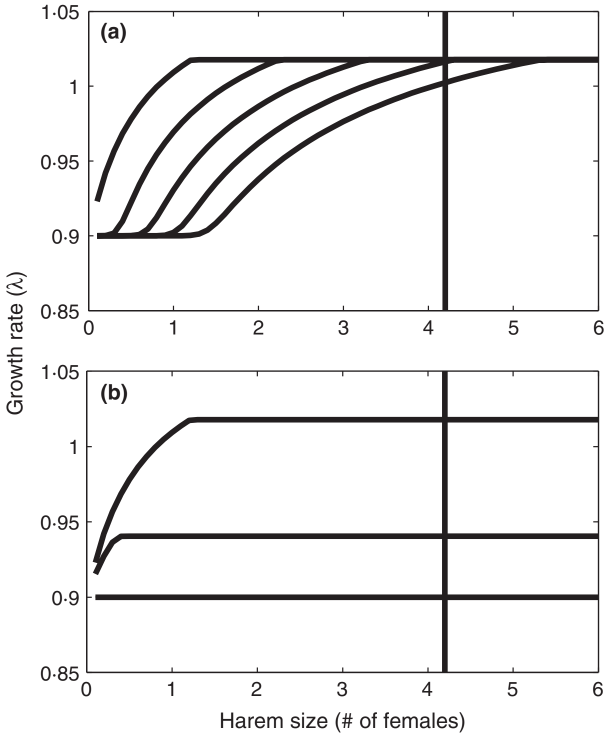

Fig. 2. Population growth rate (λ) as a function of harem size. Both figures represent results for the modified harmonic fecundity equation. The vertical line designates the harem size estimated from field data. (a) Assumes a constant survival rate for adult females at 0·9 where the five lines designate changes in adult male survival rate from 0·9 to 0·5, top to bottom, respectively. (b) Assumes a constant survival rate for adult males at 0·9 where the five lines designate changes in adult female survival rate from 0·9 to 0·5. Note that the bottom three lines here overlap one another.

Table 3. Comparison of simulation model results to empirical parameter estimates

	Rank	End Pop. Size	Growth rate (λ)	Stage distribution			
				Pups	Juveniles	Adult males	Adult females
Two-sex (MHFF)	1	1638* (341–2899)	1·076 (1·047–1·104)	0·296* (0·270–0·323)	0·138* (0·124–0·151)	0·243 (0·173–0·313)	0·323 (0·289–0·357)
Two-sex	2	888* (350–1429)	1·053 (1·031–1·075)	0·263 (0·259–0·267)	0·125* (0·116–0·134)	0·246 (0·190–0·305)	0·366 (0·306–0·422)
One-sex	3	1281* (138–2424)	1·054 (1·023–1·086)	0·262 (0·256–0·268)	0·124 (0·111–0·136)	NA	0·614 (0·602–0·626)
Two-sex (HFF)	4	3889 (949–6875)	1·108 (1·080–1·137)	0·341 (0·325–0·357)	0·153 (0·142–0·164)	0·218* (0·161–0·274)	0·289 (0·250–0·328)
Actual population census (for one-sex)		430 (284)	1·018 (1·019)	0·276 (0·218)	0·132 (0·105)	0·161 (NA)	0·431 (0·677)

Mean values and (95% CI) are given for each measurement. Where field estimates fall within the 95% CI of simulation estimates is indicated by *. The last row provides estimates of each measurement from census data with () denoting the measurement used for comparison to the one-sex model.

stage class over the 30-year time series of a particular simulation. After 1000 simulations, a distribution for the proportion of individuals in each stage could be calculated. We evaluated model fit for stage distributions with the same method used for population growth rates and end population size. Table 3 shows the rank order of models according to how many measurements, or patterns, each model fits when compared to field data.

Results

EQUILIBRIUM AGE STRUCTURE AND POPULATION GROWTH RATE (λ)

Our analysis of the extent to which one- and two-sex models differ with respect to equilibrium age structure shows that when survival rates are equal, the equilibrium age structure includes an equal number of females and males (Fig. 1). Although our two-sex model is frequency-dependent, it depicts a population at SAD and grows exponentially according to the largest eigenvalue (λ) of the equilibrium projection matrix. This means that the standard metric λ is adequate for describing population growth for such models. Our estimates of λ are similar, with the two-sex harmonic fecundity model producing the highest growth rate followed by the modified harmonic model (Table 2). The two-sex model with a scalar value for fertility and the one-sex model generate the lowest growth rates.

In examining the relevance of harem size and survival rates on λ (Fig. 2), we found that, to achieve positive population growth, adult female survival rate must be high regardless of harem size (Figs 2 & 3). To achieve positive population growth with our modified harmonic fertility,

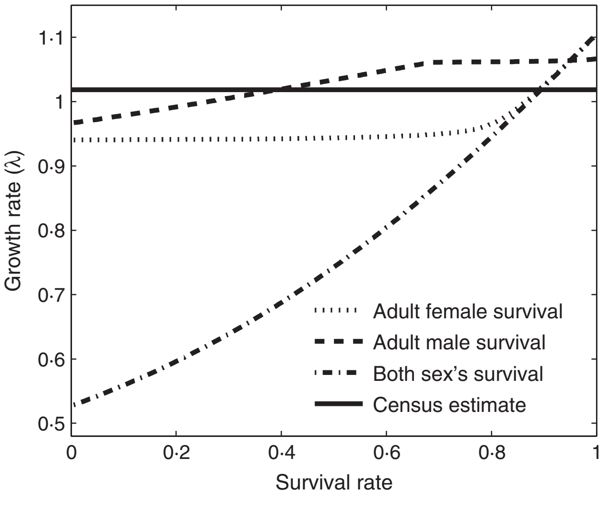

Fig. 3. Population growth rate (λ) for changes in survival rates of adult males (male), adult females (female) or both. As we allow one sex's survival rate to vary, the other sex has a constant survival rate of 0·95 (the best estimate of adult survival rate). Note that where the three curves intersect, both adult male and female survival rates are at the default value of 0·95. For reference, we show an independent estimate of λ (solid horizontal line), estimated from census data (1·0184).

adult female survival rate had to be at least 0·9 with a male survival rate of 0·5 (see Fig. 3). This is quite a bit different than the two-sex model with scalar births (equivalent to one-sex case when survival rates are equal). In the scalar births case, either sex could have a survival rate of 0·05 as long as the other sex had a survival rate of at least 0·95. Alternatively, survival rates could be equal across sexes at a value of 0·9 to insure positive population growth. These results suggest that for polygynous species, assuming equal survival rates for both sexes could be misleading.

ELASTICITIES

Patterns of elasticity vary only slightly for one- and two-sex models (Table 2). Elasticities in the two-sex cases are equal only when sex ratio is unity, which in our example occurs when adult survival rates are the same for both sexes. In the one-sex case (density-independent), a change in a vital rate may change the SAD, but it does not change other rates mediated by changes in SAD. In contrast, for two-sex models, a change in a vital rate may lead to changes in other vital rates (e.g. a change in survival leads to a change in fertility because fertility depends on the SAD). When male survival is higher than female survival, the two-sex model predicts smaller elasticities for female survival than the one-sex model. This is because female survival is already high and increasing male survival produces a larger change in growth rate than increasing female survival. When female survival is higher than male survival, the two-sex model predicts much higher elasticity for female survival than the one-sex model, reflecting the influence of female survival on population growth rate.

EXTINCTION RISK

Our two-sex model with the non-modified fertility function predicted the lowest risk of extinction (Fig. 4). Both the one-sex and two-sex models (with scalar births) predicted a higher estimate of extinction risk, while the two-sex model with the modified fertility function fell in the middle for extinction risk (Fig. 4).

MODEL EVALUATION

To evaluate the success of each of our models, we made six measurements to compare to analogous census data: growth rate, end population size and stage distribution of pups, juveniles, adult males and adult females. The two-sex model with the modified HFF performed the best (i.e. matched the highest number of measurements, with a maximum value of six), followed by the two-sex model with scalar births (Table 3). Both the one-sex and two-sex model with the non-modified HFF performed the poorest when compared to the field estimates of our six measurements.

Discussion

The vital rate estimates necessary to parameterize two-sex models may be expensive and difficult to obtain in wild populations, so it is important to identify when such additional estimates are cost-effective. We have demonstrated that there are situations in which two-sex models are more appropriate than the commonly used female-based model. In particular, our results suggest that two-sex models are relevant in cases where vital rates for sexes differ (Figs 1 & 3) and in polygamous species such as sea lions (Fig. 2). We recognize that for many imperilled species, vital rates are not available and immediate management actions must be taken. In addition to tackling such ‘small population crises’, we must also develop approaches to ensure long-term persistence (Caughley 1994). Our sea lion case study is one step in this direction.

These results underscore the need for estimates of vital rates for the complete life cycle for California sea lions.

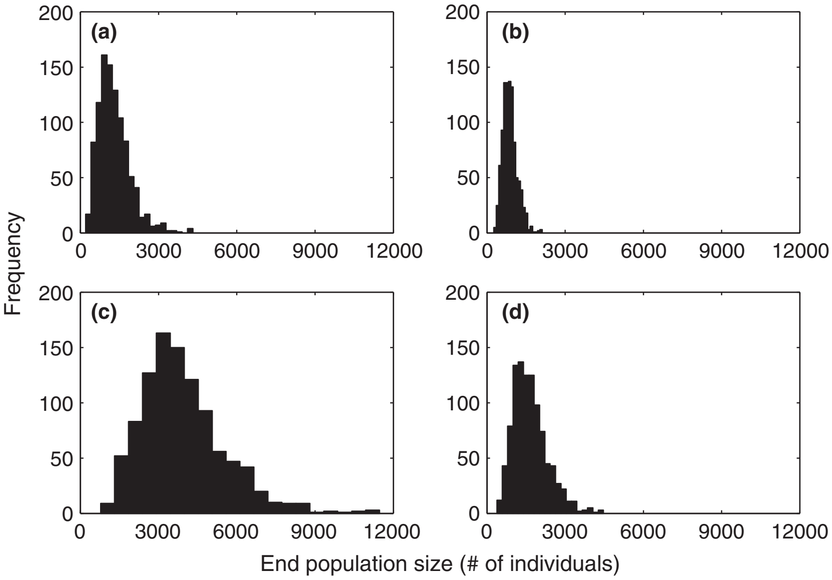

Fig. 4. Frequency distribution resulting from Monte Carlo simulations of population size after 30 years. (a) Represents results from the one-sex model (μ = 1336, σ = 602); (b) represents results from the two-sex model with births set at a scalar value (μ = 899, σ = 283); (c) Represents results from harmonic fecundity model (μ = 3966, σ = 1543); (d) represents results from modified harmonic fecundity model (μ = 1677, σ = 689).

Such demographic data will allow the development of suitable models used to develop management recommendations and ensure the population persistence. Conservation plans for California sea lions in Mexico currently manage the entire Gulf as a unique demographic unit (Szteren, Aurioles & Gerber 2006). Our results suggest that a more detailed demographic structure should be considered in developing management strategies. For example, it will be important to identify sex-specific response to disturbance to develop management practices regarding marine mammal interactions with humans, such as vessel speed reductions, prohibited areas (time and area closures) and tourist operator licensing. These insights may be used to develop general principles for the use of two-sex models in assessing population viability. While these principles emerge from our analysis of sea lion data, we expect that our conclusions are broadly applicable to other species with similar life histories.

TWO-SEX MODELS SHOULD BE DEVELOPED FOR POPULATIONS FOR WHICH VITAL RATES VARY BETWEEN MALES AND FEMALES

Mortality rates can differ between sexes as a result of sexual selection, mating system or environmental variation. Many polygynous species (e.g. red deer, Clutton-Brock, Guinness & Albon 1982; Owen-Smith 1993) show sexual dimorphism in size, which results in males having higher mortality rates at some or all ages. Differences in mortality for adult ages lead to a skewed ratios in favour of the sex with lower mortality (Fig. 1). Population models for species with sex-specific vital rates should include accurate estimates of such vital rates. For our case study, while female survival rate is more important than male survival rate in promoting population growth, a high male survival could compensate for low female survival (Fig. 3). However, as female survival declines, male survival becomes increasingly important. This insight emerges from our use of the HFF to model a polygamous species. These results could be used to establish sex-specific recovery goals (e.g. to achieve $\lambda > 1$, a decline in female survival from 0·95 to 0·9 could be offset by an increase in male survival from 0·3 to 0·5).

TWO-SEX MODELS SHOULD BE DEVELOPED FOR POPULATIONS THAT EXHIBIT BIASES IN SEX RATIO

In our analysis, we used a simple two-sex model (Caswell & Weeks 1986; Lindström & Kokko 1998) where fertility is assumed to depend on the fractions of adult males and females for the harmonic fecundity function. Recent work (Veran & Beissinger 2009) has highlighted the importance of demographic and ecological factors (difference in juvenile mortality, sex-biased dispersal) on adult sex ratio. Skewed sex ratio may result from environmental variation (e.g. incubation temperature determines sex in American alligator, Ferguson & Joanen 1982), population density (red deer, Loeske *et al.* 1999) and predation (e.g. predation by herons affects sex ratios in natural populations of the mosquito fish *Gambusia affinis*, Britton & Moser 1982) among other factors. As discussed above, differences in male and female vital rates may also lead to a skewed sex ratio (Fig. 1). Our results illustrate how biases in sex ratio may influence the response of long-term growth rate to small changes in vital rates (Fig. 3). A two-sex model may produce different dynamics than a female-only density-independent model if sex ratio is different from one. One conclusion derived from our analyses is that reliable estimates of sex ratio are essential for determining the importance of using two-sex models.

TWO-SEX MODELS SHOULD BE DEVELOPED FOR SPECIES WITH POLYGYNOUS AND POLYANDROUS MATING SYSTEMS

In mating systems with harems, female fertility becomes more important than survival because females may compete with each other for mating. For PVA, this implies that vital rates targeted for management may respond differently depending upon the mating system. We show that for a polygynous species like California sea lions, accurate estimates of operational sex ratio (estimated here as harem size) appear to be an important parameter in demographic PVA models because operational sex ratio affects the growth rate of the population (Fig. 2). In addition, because we use a HFF, female survival rate must be high to ensure positive population growth (Fig. 3). We also find that population growth is relatively insensitive to changes in male survival rate as long as female survival rate is high. However, when survival rate is low for both sexes, male survival rate becomes more important (Fig. 3).

WHEN TWO-SEX MODELS ARE DEVELOPED, ELASTICITY ANALYSIS SHOULD BE CONDUCTED ON SEX-SPECIFIC VITAL RATES

Our analyses illustrate how biases in sex ratio may influence the response of the long-term growth rate to small changes in vital rates (Fig. 3). We have shown that elasticities of vital rates depend upon the sex ratio and reflect the response of population growth to sex-specific perturbations. However, these results do not take into account the variation in vital rates, as they were not available for this population; this variation can dramatically affect results and conservation actions (Mills, Doak & Wisdom 1999). When male mortality is higher than female mortality, increasing male survival may be more advantageous than increasing female survival (Fig. 3). Hence from a PVA point of view, managers may also want to focus on improving male vital rates in conservation efforts, especially when female survival rates are already high (Fig. 3). However, although our elasticity measures indicate that male and female survival rates are important for conservation, there would be little that could be done to increase these survival rates. The adult sea lions at our study site have an estimated 0·95 probability of survival leaving very little room for improvement. In this case, it may be better to focus on other segments of the population that also play a significant role in contributing to the overall growth rate (e.g. survival of juveniles). Of course, if the goal were simply to maintain the current increase in population trend, then the first objective would be to ensure continued high survival rates of adult males and females. It may be more effective to conserve the males over the females based on the growth rates produced with different combinations of survival rates (Fig. 3). Determining bounds by which survival rates could drop or need to be raised to in order to ensure positive population growth can also help in management decisions (Fig. 3).

CONCLUSION

The importance of including details on male vital rates in population models used in conservation has been underestimated. In this paper, we show that a two-sex model can produce different dynamics than a female-only density-independent model if sex ratio is different than one. The level of polygyny can affect the overall population growth rate (Fig. 2). For PVA, this implies that vital rates targeted for management would respond differently depending upon the mating system. Furthermore, two-sex models generally yield lower extinction risks than one-sex models (Fig. 4). However, we also found that two-sex models more accurately describe the long-term trends in distribution and population size (Table 3). This suggests that two-sex models should be developed for populations that exhibit biases in sex ratio, and underscores the importance of including accurate estimates of sex-specific vital rates in population models used in conservation (Fig. 3). While we use sea lions as an example, we simulated a variety of situations where male and female survival rates are different (Figs 1, 2 & 3). Thus, as long as sexual dimorphism in adult mortality produces long-term skewed sex ratios, our results on sensitivities may apply generally across other taxa. That is, sensitivities calculated from female-only PVA models will be different from those of two-sex calculations. Vital rates targeted for management may respond differently for males and females and for different assumptions about sex ratio. Thus, conservation biologists should carefully consider the social structure and sex ratio of focal species in order to determine whether a two-sex matrix model will yield more accurate estimates of extinction risk than standard one-sex models.

Acknowledgements

We would like to thank José Daniel Anadón, Jesse Senko, Robert Wildermuth, Marc Cadotte and two anonymous reviewers for their comments on our manuscript. E.R.W. was partially funded by the School of Life Sciences Undergraduate Research Program at Arizona State University.

References

Akcakaya, H.R., Radeloff, V.C., Mladenoff, D.J. & He, H.S. (2004a) Integrating landscape and metapopulation modeling approaches: viability of the sharp-tailed grouse in a dynamic landscape. *Conservation Biology*, **18**, 526–537.

Akcakaya, H.R., Burgman, M.A., Kindvall, O., Wood, C.C., Sjogren-Gulve, P., Hatfield, J.S. & McCarthy, M. (2004b) *Species Conservation and Management: Case Studies*, pp. 533. Oxford University Press, New York, USA.

Akcakaya, H.R., Franklin, J., Syphard, A.D. & Stephenson, J.R. (2005) Viability of Bell's sage sparrow *(Amphispiza belli* ssp. *Belli*): altered fire regimes. *Ecological Applications*, **15**, 521–531.

Anthony, L.L. & Blumstein, D.T. (2000) Integrating behaviour into wildlife conservation: the multiple ways that behaviour can reduce N_e. *Biological Conservation*, **95**, 303–315.

Austad, S.N. (2011) Sex differences in longevity and aging. *Handbook of the Biology of Aging*, 7th edn, (eds E.J. Masoro & S.N. Austad), pp. 479–496. Academic Press, San Diego.

Bain, L.J. & Engelhardt, M. (1991) *Introduction to Probability and Mathematical Statistics*. Duxbury Press, Pacific Grove, California, USA.

Barrett, S.C.H. & Hough, J. (2013) Sexual dimorphism in flowering plants. *Journal of Experimental Botany*, **64**, 67–82.

Beaudry, F., deMaynandier, P.G. & Hunter, M.L. (2008) Identifying road mortality threat at multiple spatial scales for semi-aquatic turtles. *Biological Conservation*, **141**, 2550–2563.

Beissinger, S.R. & Westphal, M.I. (1998) On the use of demographic models of population viability in endangered species management. *The Journal of wildlife management*, **82**, 1–841.

Bell, G. (1980) The costs of reproduction and their consequences. *American Naturalist*, **116**, 45–76.

Bretagnolle, V. & Inchausti, P. (2005) Modelling population reinforcement at a large spatial scale as a conservation strategy for the declining little bustard *(Tetrax tetrax)* in agricultural habitats. *Biological Conservation*, **122**, 375–384.

Britton, R.H. & Moser, M.E. (1982) Size specific predation by herons and its effect on the sex-ratio of natural populations of the mosquito fish *Gambusia affinis* baird and girard. *Oecologia*, **53**, 146–151.

Carey, J.R., Liedo, P. & Vaupel, J.W. (1995) Mortality dynamics of density in the Mediterranean fruit fly. *Experimental Gerontology*, **30**, 605–629.

Caswell, H. (2001) *Matrix Population Models. Construction, Analysis, and Interpretation*. pp. 564. Sinauer, Sunderland.

Caswell, H. (2008) Perturbation analysis of nonlinear matrix population models. *Demographic Research*, **18**, 27–83.

Caswell, H. & Weeks, D.E. (1986) Two-sex models: chaos, extinction, and other dynamic consequences of sex. *American Naturalist*, **128**, 707–735.

Caughley, G. (1994) Directions in conservation biology. *Journal of Animal Ecology*, **63**, 215–244.

Chirakkal, H. & Gerber, L.R. (2010) Short and long-term population response to changes in vital rates: implications for demographic population viability analysis. *Ecological Applications*, **20**, 783–788.

Clutton-Brock, T.H., Guinness, F.E. & Albon, S.D. (1982) *Red Deer: Behavior and Ecology of Two Sexes*. University of Chicago Press, Chicago, IL, USA.

Delph, L.F. (1999) Sexual dimorphism in life history. *Gender and Sexual Dimorphism in Flowering Plants* (eds M.A. Geber, T.E. Dawson & L.F. Delph), pp. 149–163. Springer, Berlin.

Eppley, S.M. (2001) Gender-specific selection during early life history stages in the dioecious grass, *Distichlis spicata*. *Ecology*, **82**, 2022–2031.

Ferguson, M.W.J. & Joanen, T. (1982) Temperature of egg incubation determines sex in *Alligator mississippiensis*. *Nature*, **296**, 850–853.

Flatz, R., Young, J.K., González-Suárez, M., Young, J.K., Hernández, C.J., Immel, A.J. & Gerber, L.R. (2012) Weak polygyny in California sea lions and the potential for alternative mating tactics. *PLoS ONE*, **7**, e33654.

Gerber, L.R. (2006) Including behavioral data in demographic models improves estimates of population viability. *Frontiers in Ecology and the Environment*, **4**, 419–427.

Guichón, M.L. & Doncaster, C.P. (2008) Invasion dynamics of an introduced squirrel in Argentina. *Ecography*, **31**, 211–220.

Hamel, S., Cote, S.D., Smith, K.G. & Festa-Bianchet, M. (2006) Population dynamics and Harvest potential of mountain goat herds in Alberta. *The Journal of Wildlife Management*, **70**, 1044–1053.

Harveson, P.M., Lopez, R.R., Lilvy, N.J. & Frank, P.A. (2004) Source--sink dynamics of Florida key deer on big pine key, Florida. *The Journal of Wildlife Management*, **68**, 909–915.

Hernández-Camacho, C.J., Aurioles-Gamboa, D., Laake, J. & Gerber, L.R. (2008) Survival rates of the California sea lion, *Zalophus californianus*, in Mexico. *Journal of Mammalogy*, **89**, 1059–1066.

Le Galliard, J.F., Fitze, P.S., Ferriere, R. & Clobert, J. (2005) Sex ratio bias, male aggression, and population collapse in lizards. *Proceedings of the National Academy of Sciences, U S A*, **102**, 18231–18236.

Legendre S. (2004) Influence of age structure and mating system on population viability. *Evolutionary Conservation Biology* (eds R. Ferrière, U. Dieckmann & D. Couvet), pp. 41–58. Cambridge University Press, Cambridge.

Lindström, J. & Kokko, H. (1998) Sexual reproduction and population dynamics: the role of polygyny and demographic sex differences. *Proceedings of the Royal Society, Series B*, **265**, 483–488.

Loeske, E.B., Kruuk, L.E.B., Clutton-Brock, T.H., Albon, S.D., Pemberton, J.M. & Guinness, F.E. (1999) Population density affects sex ratio variation in red deer. *Nature*, **399**, 459–461.

Ludwig, D. & Walters, C.J. (1985) Are age-structured models appropriate for catch-effort data? *Canadian Journal of Fisheries and Aquatic Sciences*, **42**, 1066–1072.

Meagher, T.R. & Antonovics, J. (1982) The population biology of *Chamaelirium luteum*, a dioecious member of the lily family: life history studies. *Ecology*, **169**, 0–1700.

Miller, T.E.X. & Inouye, B.D. (2011) Confronting two-sex demographic models with data. *Ecology*, **92**, 2141–2151.

Mills, L.S., Doak, D.F. & Wisdom, M.J. (1999) Reliability of conservation actions based on elasticity analyses of matrix models. *Conservation Biology*, **13**, 815–829.

Milner-Gulland, E.J., Bukreeva, O.M., Coulson, T., Lushchekina, A.A., Kholodova, M.V., Bekenov, A.B. & Grachev, I.A. (2003) Reproductive collapse in saiga antelope harems. *Nature*, **422**, 135.

Morris, W.F. & Doak, D.F. (2002) *Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis*, pp. 200–220. Sinauer Associates, Inc., Sunderland, MA, USA.

Owen, C. (2008) *Parameter estimation for the beta distribution*. Master's Thesis, Brigham Young University.

Owen-Smith, N. (1993) Comparative mortality rates of male and female kudus: the costs of sexual size dimorphism. *Journal of Animal Ecology*, **62**, 428–440.

Promislow, D.E.L. (1991) Senescence in natural populations of mammals: a comparative study. *Evolution*, **45**, 1869–1887.

Rankin, J. & Kokko, H. (2007) Do males matter? The role of males in population dynamics. *Oikos*, **116**, 335–348.

Ray, C., Gilpin, M. & Smith, A.T. (1991) The effect of conspecific attraction on metapopulation dynamics. *Biological Journal of the Linnean Society*, **42**, 123–134.

Robinson, H.S., Wielgus, R.B., Cooley, H.S. & Cooley, S.W. (2008) Sink populations in carnivore management: cougar demography and immigration in a hunted population. *Ecological Applications*, **18**, 1028–1037.

Shelton, A.O. (2010) The ecological and evolutionary drivers of female--biased sex rations: two-sex models of perennial seagrasses. *American Naturalist*, **175**, 302–315.

Sutherland, W.J. & Norris, K. (2002) Behavioral models of population growth rates: implications for conservation and prediction. *Philosophical Transactions of the Royal Society of London Series B—Biological Sciences*, **357**, 1273–1284.

Szteren, D., Aurioles, D. & Gerber, L.R. (2006) Population status and trends of the California sea lion (*Zalophus californianus californianus*) in the Gulf of California, México. *Sea Lions of the World: Conservation and Research in the 21st Century* (eds A. Trites, S. Atkinson, D. DeMaster, L. Fritz, T. Gelatt, L. Rea & K. Wynne), pp. 369–384. Alaska Sea Grant College Program, University of Alaska Fairbanks, Fairbanks, Alaska.

Veran, S. & Beissinger, S.R. (2009) Demographic origins of skewed operational and adult sex ratios: perturbation analyses of two-sex models. *Ecology Letters*, **12**, 129–143.

Ward, E.J., Chirakkal, H., González-Suárez, M., Aurioles-Gamboa, D., Holmes, E.E. & Gerber, L. (2009) Inferring spatial structure from time-series data: using multivariate state-space models to detect metapopulation structure of California sea lions in the Gulf of California, Mexico. *Journal of Applied Ecology*, **47**, 47–56.

Wielgus, J., Gonzalez-Suarez, M., Aurioles-Gamboa, D. & Gerber, L.R. (2008) A Noninvasive demographic assessment of sea lions based on stage-specific abundances. *Ecological Applications*, **18**, 1287–1296.

Wintle, B.A., Bekessy, S.A., Venier, L.A., Pearce, J.I. & Chisolm, R.A. (2005) Utility of dynamic-landscape metapopulation models for sustainable forest management. *Conservation Biology*, **19**, 1930–1943.

Young, J.K., Gonzalez-Suarez, M. & Gerber, L.R. (2008) Determinants of agonistic interactions in California sea lions. *Behavior*, **145**, 1797–1810.

Received 3 March 2013; accepted 19 September 2013
Handling Editor: Marc Cadotte