Including behavioral data in demographic models improves estimates of population viability

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Individual differences in behavior and social status can determine the rate of population change and thus the threat that imperiled species face in the real world. One way that behavior may be manifested in terms of an annualized population growth rate (λ) is through the effects of sex ratio biases. A population's operational sex ratio (OSR) typically deviates from the actual sex ratio (ASR), leading to pronounced sexual dimorphism in fecundity. This paper provides a framework for integrating behavioral estimates of OSR into population models used for conservation. Male and female fertility is estimated at six island study sites for California sea lions (*Zalophus californianus*), using population census data (ASR) and behavioral data (OSR). These estimates are used to construct alternate projection matrices to examine the impacts on λ. Inclusion of behavioral data in population models not only allows for explicit analysis of the effects of behaviors on viability, but may also help to identify behavioral attributes that could be used as an early indicator of population decline.

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The integration of behavioral ecology and conservation biology attracted a great deal of attention in past years (Curio 1996; Caro 1998; Sutherland 1998). While there has been wide recognition that behavior can profoundly influence the dynamics of populations (Sutherland 1996; Houston and McNamara 1997), empirical research linking behavior to demography is sparse (Anholt 1997; Levin *et al.* 2000). Furthermore, a framework for applying behavioral knowledge to real-world conservation problems has not yet been developed (Anthony and Blumstein 2000). Individual behavioral strategies influence how animals respond to perturbation, so understanding factors that influence behavior over short time scales may provide important information for developing accurate population models (Sutherland 1988; Durant 1998).

In a nutshell:

- Individual differences in behavior and social status can determine the rate of population change and thus the threat that imperiled species face in the real world
- An approach to integrate behavioral estimates of operational sex ratio into population models used for conservation is presented here
- Vital rates are estimated for sea lions (*Zalophus californianus*) at six island study sites in the Gulf of California based on both population and behavioral data; these estimates are used to construct alternate projection matrices to examine the impacts of behavior on population growth
- Behaviorally based proxies of demographic population viability could serve as an "early warning system" for conservation practitioners, potentially circumventing expensive and time-consuming population data collection efforts

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Theory about small populations suggests a number of potential links between behavior and population viability, as mediated by a population's sex ratio (Anthony and Blumstein 2000). Specifically, a species' mating system dictates the similarity between the actual sex ratio (ASR) and the operational sex ratio (OSR) of the population. While the ASR reflects the true ratio of females to males, the OSR is the ratio of breeding females per breeding male. These sex-based differences are typically ignored in population models used for conservation, since only the female portion of the population is explicitly modeled. The assumption is that only females determine the population growth rate. In theory, the mating system links behaviors such as mate defense and territoriality indirectly to population growth via the difference between ASR and OSR. Here, I distinguish between genetic and demographic measures of population viability and argue that the link between behavior (mediated through the OSR) and demographic population viability cannot be ignored.

Population geneticists typically quantify the genetic viability of a population using the mean and variance of successful gametes per individual as a proxy for genetic variability (Lande 1994). By this measure, small populations with biased sex ratios have lower genetic viability than populations with even sex ratios of the same population size. By contrast, population biologists typically assess the demographic viability of a population based exclusively on means and variances in female fecundity, survival, and abundance. This assumes either that these parameters are similar for males, or that in males they

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simply do not matter. Either assumption would lead a conservation biologist to suppose that the number of males present in a population is of little interest provided all females are mated.

Here, I challenge this assumption and provide a quantitative framework for testing hypotheses that link behavior to demographic population viability. For simplicity, I use a very general measure of demographic viability – the population growth rate, λ. This forms the cornerstone of most population viability analyses based on projection matrices (Doak *et al.* 1994; Heppell *et al.* 1996; Caswell 2001). Other measures may indeed be better or more appropriate in some situations, depending on the particular application of behavioral research for conservation.

Using field data on California sea lion (*Zalophus californianus*) behavior from six island breeding sites, I estimate male and female fecundity via theoretical relationships between fecundity and sex ratio and then use them in a 2-sex matrix model to calculate population growth rate (ie demographic population viability). I contrast population viability when λ is estimated with ASR and OSR. OSR can only be determined empirically via direct observation of mate defense or via more detailed genetic analyses. Values of λ are then compared to those generated from time series of population abundance data for each site (Dennis *et al.* 1991). Time series of abundance data provide a valuable control against which to compare estimates of demographic viability from matrix models parameterized with behavioral data. The general applications of this approach are twofold: (1) the models can be used to test basic hypotheses about how behavior may modify demographic population viability (hereafter referred to as viability), and (2) the models provide a framework for identifying key behavioral attributes of viability for use as an early indicator of population decline.

Male fecundity – a forgotten ingredient of small population viability

Mating systems provide a potentially unifying framework for integrating genetic and demographic perspectives on population viability. While the effect of small population size on mating success has been considered in the context of Allee effects for small populations (Abrams 2002), few viability models include behavioral variation (Derrickson *et al.* 1998; Anthony and Blumstein 2000). Moreover, the extent to which biases in OSR determine population growth (especially in small populations) is even less clear. For monogamous animals, female biased sex ratios are clearly a demographic liability, whereas in polygynous animals, this may actually improve the viability of a small population, relative to a population of the same size with a 1:1 sex ratio. However, even for animals that have adopted mating systems with strongly biased sex ratios, social dysfunction and reproductive collapse may occur when bias exceeds critical thresholds (Milner-Gulland 2003). This suggests a more complex relationship between the demographic consequences of bias in sex ratios and the viability of a population.

While sex ratio is an important parameter in the demography of animal populations (LeGalliard *et al.* 2005), the influence of individual variation on population dynamics remains poorly understood. Territorial behavior exhibited by male animals during the breeding season greatly influences the number of males copulating with females and thus siring young. Recent empirical evidence suggests that at extreme biases in male sex ratio and small population size, the number of males in a population is related to female fecundity (Millner-Gulland 2003; LeGalliard *et al.* 2005). For example, an extremely low proportion of males in a population of saiga antelope (*Saiga tatarica tatarica*) led to sharp declines in abundance (Milner-Gulland 2003), because dominant females prevented young females from breeding with the rare males. Similarly, an excess of adult males of the common lizard (*Lacerta vivipara*) causes aggression towards adult females, whose survival, fecundity, and emigration subsequently decline (LeGalliard *et al.* 2005). This suggests that, consistent with genetic definitions of viability, extinction risk (ie demographic viability) may be influenced by both positive and negative biases in sex ratio. In either case, OSR is an indirect way of incorporating behavior into population models.

I would suggest that the effect of sex ratio on the viability of small populations depends strongly on the mating system of the focal species. Specifically, when populations are small, males become limiting, and this may influence viability. Furthermore, the way in which sex ratio is included in population models may have profound impacts on viability estimates. The extent to which variation in male reproductive success actually matters for population growth (λ) is discussed below, using territoriality in male reproductive success in sea lions as a case study.

Mating systems and conservation

Three cornerstones of behavioral ecology are predator–prey interactions, cooperation and conflict, and mating systems (Krebs 1984; Alcock 2001). Mating systems offer an interesting opportunity to examine the intersection between behavior and population biology because of the variable effects on male and female fertility. Mating system dynamics may influence a population's vulnerability to harvest and may therefore determine why some populations have recovered and others have gone extinct. For example, there may be upper and lower thresholds in a population's sex ratio (f:m) which, when exceeded, result in reproductive collapse (Milner-Gulland 2003).

Behavioral options for reproduction are diverse (Table 1); any mating system is an assortment of some subset of these possible options. In light of the large number of permutations, defining different mating systems is not straightforward (Alcock 2001). In general, mating systems have been distinguished based on (1) the number of individuals with which a male or female copulates; (2)

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Table 1. Overview of mating system theory

Mating system	*Behavioral strategies*	*Which sex has higher variation in fertility*	*Examples*
Male assistance monogamy	Male assists mate	Equal	Most birds (Lack 1968), wolves (Mech 1970)
Mate guarding monogamy	Male guards mate	Low	Black headed gull (Alcock 2001)
Sperm replenishment polyandry	Females mate with multiple males to secure additional sperm	Females	Drosophila fruit flies (Page 1980)
"Prostitution" polyandry	Females mate with multiple males to gain access to resources	Females	Hummingbirds (Wolf 1975)
Resource defense polyandry	Males assume most parental duties and compete for mates	Females	Spotted sandpiper (Maxson 1980), jacana (Jenni 1974)
Lek polyandry	Females compete for dominance position because males select high ranking females	Females	Northern phalarope (Emlen 1977)
Female defense polygyny	Male defends harem	Male	Gorillas (Harcourt 1981), lions (Schaller 1972), tropical bats (Alcock 1984)
Scramble competition polygyny	Non-territorial search for mates	Male	Wood frog (Alcock 1984)
Resource defense polygyny	Male defends resources	Male	Impalas (Jarman 1979), desert woodrats (Vaughan 1980)
Lek polygyny	Males defend symbolic territory	Male	White-bearded manakin (Alcock 1984)

Mating systems are determined by ecological factors that determine a male's potential to monopolize mates or assist in producing and rearing offspring (following Alcock 1984). These behavioral strategies may in turn influence population parameters such as variation in fertility.

whether a male and a female form a pair bond and cooperate in parental care; and (3) how long the pair bond is maintained (Alcock 2001). However, the number of combinations of these variables is substantial. Alcock (2001) suggests restricting classification of mating systems to the first criterion only. In other words, there are two strategies for each sex: to mate with just one partner per breeding period (male and female monogamy) or to copulate with several different individuals (male polygyny and female polyandry). Table 1 provides an overview of mating system theory and Table 2 shows the extent to which each strategy influences population parameters such as variation in fertility. Hypothesized effects of each behavior on λ for male sea lions include factors such as female encounter rate, fertilization rate, and territory defense. Identifying the extent to which these mating options determine population viability for a variety of taxa may be important to the conservation of biodiversity. Quantitative analyses of the relative rank of the contribution of each behavioral option may allow identification of those that are most critical to determining variation in population parameters.

Among the diversity of mating options, territoriality is one strategy that may have a profound impact on a population's sex ratio (ie if only a small fraction of males are breeding). Territoriality may also influence other parameters that are important for population viability. For example, among yellow-bellied marmots (*Marmota flaviventris*), there is considerable variation in the number of females occupying a male's territory, such that the average annual reproductive success of a female actually declines as group size increases (Downhower and Armitage 1971). In polygynous mammals such as sea lions, male reproductive success is largely determined by the number of females present in their territory; males compete for mates and females invest in parental care (Trivers 1972). Territorial behavior is likely to be of particular relevance for population dynamics in polygynous populations, resulting in biased OSRs.

Behavioral–demographic models

A number of useful tools have been developed to measure the potential effects of variation in vital rates on population growth (Doak *et al.* 1994; Gerber and DeMaster 1999; Gross 2000). Central to all is the simple Leslie matrix model (Leslie 1945) which is typically applied only to the female portion of the population (Caswell 2001), and consequently allows for examination of causal relationships between female vital rates and population growth. Few matrix models consider male vital rates and abundance, and none explicitly incorporate behavior in this context (Stephens *et al.* 2002).

Simple (1-sex) Leslie matrix models can easily be extended to accommodate both sexes (ie male and female

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Table 2. Examples of behavioral options for increasing population viability (following Krebs 1984)

Attribute of population viability for males	*Behavioral options for increasing population viability*	*Hypothesized effect on λ for sea lions*
Female encounter rate	Increase proximity to female resources	Low
	Increase proximity to sites ideal for displaying to attract females	High
	Search for females (randomly or using cues)	Low
	Remain with females once encountered	Moderate
Fertilization rate	Exclude other males by territoriality	High
	Exclude other males by dominance	Moderate
	Tolerate other males but control order or timing of insemination	Low
	Guard female after insemination	Low
Female fecundity	Select preferred mates using size or age as cue	Moderate
Juvenile survival	Select females of appropriate age, size, status	Low
	Invest in territoriality, parental care, mate survival	High
Adult survival	Defer breeding to later ages	High
	Reduce investment in activities that increase risk	Low
	Defend territory for own access to resources	High
	Form social liaisons to share risks and costs	Low

vital rates) as well as explicit functions that link behavioral data to population dynamics via structured population models. Variation in vital rates between males and females is well documented for many species (Caswell 2001), including sea lions. If vital rates differ between sexes, the rate of increase for females, calculated from a single-sex matrix, may not accurately depict true patterns of population growth.

A 2-sex matrix model approach is used here to illustrate the integration of empirical data on behavior into population models of extinction risk. In particular, empirical estimates of the ASR (obtained by conducting censuses of the population at breeding sites) and OSR (based on behavioral observations of harem size) illustrate the importance of including information about mating behavior in estimates of population growth parameters. The effects of behavior on population growth are examined, using functions that relate sex-specific fecundities to sex ratio. OSR can be inferred from behavioral data that identify breeding males (those defending territories) and the number of females (ie harem size) defended by these males. For example, to examine the hypothesis that territorial behavior influences male reproductive success, one can incorporate a function that reflects the impact of breeding sex ratio on fecundity into a demographic model. With demographic schedules modified by behavior, one can then examine the impact of behavior on extinction risk. Understanding social hierarchies and territorial behavior may yield more accurate estimates of important population parameters such as male fecundity (F_m) and subadult and adult male survival ($S_{sa,m}$) – both of which directly determine λ. The resulting estimates of λ are compared to those obtained using a single-sex model with no behavior, a 2-sex model with no behavior, and independent estimates from censuses of abundance. Though more complex, the 2-sex model provides a more realistic and rigorous framework for evaluating behavioral hypotheses about demography (Caswell 2001).

Sea lions in the Gulf of California

Because of their large size, morphology, and physiology, marine mammals have been targeted in both commercial and subsistence exploitation. California sea lions (*Zalophus californianus*) have been exploited for centuries in the Gulf of California (Zavala-Gonzalez and Mellink 2000) and small-scale poaching still occurs to this day. The extent to which sea lions have recovered from past exploitation, and the demographic consequences of this exploitation, are not well understood. Sea lions are polygynous, sexually dimorphic, and form dense aggregations during breeding seasons (Berta and Sumich 1999). Sea lions are thought to exhibit site fidelity, so that populations in breeding areas (rookeries) may exhibit distinct population dynamics. During the breeding season, estrus and mating occur soon after females have given birth, and females and pups are controlled by territorial males (Boness 1991). Juveniles and subdominant males are usually excluded from breeding activities and congregate at the periphery of the rookeries. For polygynous species like sea lions, males often have delayed access to reproduction as compared to females, and have lower survival rates (Table 3). Male sea lions hold territories to gain access to females for breeding, while non-territorial males appear to contribute little to reproductive output. However, the extent to which non-territorial, "sneaker" males contribute to reproductive output is not well understood. Therefore, let us assume that the OSR is the ratio of territorial males to adult females, but also consider the possibility that non-territorial males may contribute to reproductive output (ASR).

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Synthesizing empirical data and developing population models

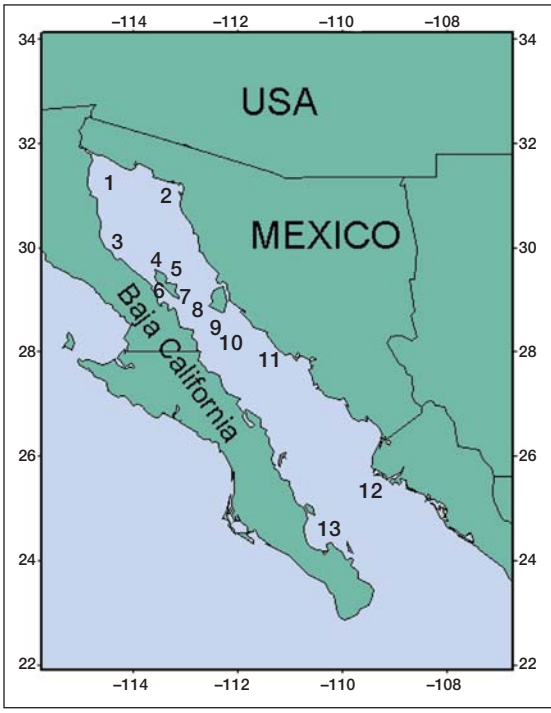
Three sources of information for sea lions in the Gulf of California are used here to illustrate a framework for integrating behavioral data into demographic analyses: (1) empirical data from a large-scale field project on sea lion behavior; (2) 30 years of population trend data for 13 island breeding sites (Gonzalez-Suarez *et al.* 2006; Szeteren *et al.* 2006); and (3) a life table constructed from 20 years of age and sex specific recapture histories for marked animals from one study site (Los Islotes Island; Hernandez 2001; Table 3). First, behavioral data are used to understand variation in activity patterns across six sites. Second, population trend data are used to estimate the population growth parameters for each study site (Figure 1). Using the Dennis *et al.* (1991) diffusion approximation (DA) method, the infinitesimal mean (μ) and variance (σ^2) of the growth rate are estimated, allowing us to evaluate probabilities for the future behavior of the populations (Figure 1). These parameters allow us to define a probability distribution that describes the likely range of λ. These independently generated distributions of λ then form the empirical foundation for model comparison, validation, and selection. At a minimum, the comparison of demographic–behavioral models to estimates from time series data provides a "best guess" using one measure, compared to several other best guesses based on matrix models.

Finally, I developed a series of matrix population models (Leslie 1945), based on estimates from sex and age-specific recapture histories of marked animals from Los Islotes island (Table 3). While these vital rates were estimated from marked animals from just one of the six island study sites, they may be used as a framework to parameterize initial mechanistic models of behavioral impacts on population dynamics. For each age category (pups, juveniles, and adults), a particular behavior may influence fecundity and survival. Because sea lions are sexually dimorphic and sexes differ in vital rates, a 2-sex matrix population model is developed, using sex-specific survival data (Table 3). A 2-sex model follows the form $n_{t+1} = A^*n_t$, where A is a transition matrix of vital rates and n is a vector of population size. Following Caswell and Weeks (1986), the model is a 39 by 39 matrix and contains two single-sex matrices: A, males and B, females. The parameter ρ depicts the adult sex ratio (here we consider both

Table 3. Model parameters (mean and standard deviation) for California sea lions

Age categories	*Age*	*Fecundity*	*Male survival*	*Female survival*
Pup	0–1	0	0.70 (0.12)	0.82 (0.04)
Juvenile	2–5	0.27 (0.19)	0.91 (0.04)	0.92 (0.07)
Subadult male	6–9	0.55 (0.04)	0.92 (0.01)	-
Adult female	6–22	0.63 (0.10)	-	0.90 (0.13)
Adult male	10–16	0	0.70 (0.34)	-

Data from Hernandez-Camacho (2001); Melin (2002); Hernandez-Camacho and Aurioles-Gamboa (2003)



Site	N	Y	μ	σ^2	λ	P_{80}	P_{ex}
Rocas Consag (1)	600	7	0.0265	0.019	1.037	0.0049	0
Isla San Jorge (2)	3833	8	0.0066	0.0043	1.009	0	0
Isla Lobos (3)	1950	7	-0.0054	0.0327	1.011	0.332	0.0007
Isla Granito (4)	246	16	-0.013	0.076	1.025	0.5094	0.1186
Los Cantiles (5)	144	21	-0.0419	0.0271	0.972	0.5774	0.0204
Los Machos (6)	102	16	-0.033	0.0407	0.987	0.3205	0.0083
El Partido (7)	82	16	-0.0197	0.1173	1.040	0.3872	0.1233
El Rasito (8)	55	20	0.0654	0.0981	1.121	0.0334	0.0061
San Esteban (9)	1748	21	0.0185	0.0257	1.032	0.0214	0
Pedro Martir (10)	247	17	0.0056	0.0695	1.041	0.1791	0.0067
Pedro Nolasco (11)	171	15	-0.0177	0.1096	1.038	0.383	0.0879
F San Ignacio (12)	58	7	-0.0176	0.038	1.020	0.2105	0.0993
Los Islotes (13)	143	21	0.0302	0.0236	1.043	0.007	0

Figure 1. *Map of study region and extinction risk estimates from 30 years of data on sea lion abundance (also see Donzalez-Suatez* et al.*, 2006; Szteren* et al. *2006) Study sites are in bold and corresponding location is indicated on map.* N *is the most recent abundance estimate,* Y *is the number of years of census data,* μ *is the infinitesimal mean of the growth rate,* σ^2 *is the variance of the growth rate,* λ *is the mean annual rate of increase, and* P_{80} and P_{ext} *are probabilities of an 80% decline and extinction over the next 50 years.*

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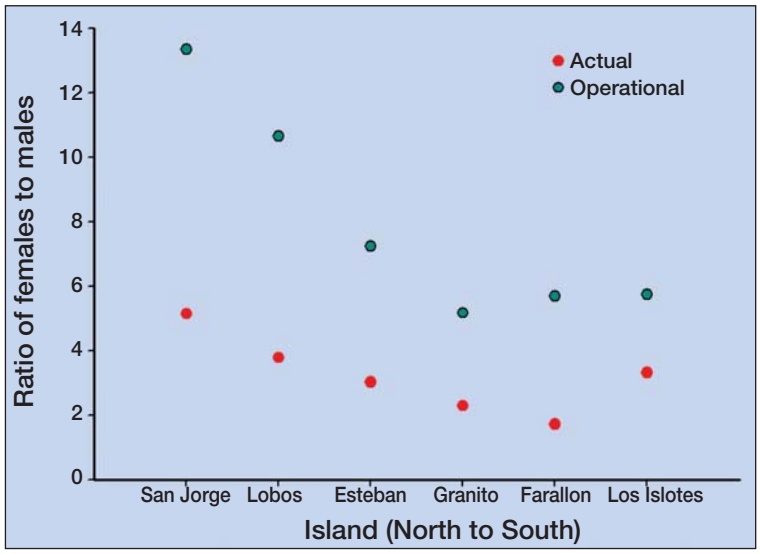

Figure 2. *(red dots) Average sex ratio for each study site; (green dots) average number of females per territory for each study site.*

ASR and OSR), P_i represents mean annual survival probabilities for age-class i, and F_A and F_B are the mean annual fertility rates for males and females, respectively. The projection matrix maps a vector of population sizes in one time unit onto the vector of population sizes in the next unit. This vector represents population size in each age class (eg the number of individuals in age classes 0, 1, 2...21) for each sex. Assuming the population is at equilibrium for age–sex composition, λ denotes the population growth rate (Caswell and Weeks 1986).

The next step is to incorporate functions that reflect mating systems into the matrix model. To do this, I use a simple function for male reproductive output, based on information about ASR and OSR. Per-capita male and female fecundities are functions of the relative abundance of males and females (Caswell and Weeks 1986; Caswell 2001). These functions summarize the demographic interaction between the sexes, and can easily be derived from the birth function, or the number of births in the population [$B_i(n)$]. Demographers and population biologists have debated the proper form of birth functions for decades (Caswell 2001). Though none are perfect, the harmonic mean birth function has persisted as the most desirable (McFarland 1972):

$$B(n) = \frac{2n_m n_f}{n_m + n_f} \quad \text{and} \quad F_m(n_m,n_f) = \frac{n_f}{n_m + n_f}$$

where $B(n)$ is the birth function and $F_m(n_m,n_f)$ is the stage-specific male reproductive output. Based on the above fertility function, the per-capita reproductive output of a male increases hyperbolically with n_f, and decreases with n_m (Caswell 2001).

With this model, we can incorporate functions relating fecundity to behavioral hypotheses in each matrix element in order to compare direct and indirect effects of behavior on vital rates. In particular, values obtained using this function may then be included in matrix elements for adult male and female fertility in the population model. Empirical data on sex ratio was used to estimate male and female fertility for each site, and these values are included in the 2-sex matrix described above. While the function for fecundity is frequency-dependent and λ does not represent population growth for models that include nonlinear functions, a particular fecundity value (constant) is estimated for each site and included in the matrix used to estimate λ. Assuming that populations are relatively small, λ provides a useful metric to compare population growth across islands. By considering λ for a small population, we can use the model to determine how fast the population will recover to pre-exploitation size.

Mapping OSR onto viability for sea lions

Empirical data for each site show that 35–58% of males do not hold territories. Primary and operational sex ratios are shown in Figure 2. Both ratios vary by site and show a decline with latitude, the northern sites exhibiting the highest sex ratios and the southern sites yielding the lowest ratios. In addition, the OSR is greater than the actual sex ratio for all sites, but the magnitude of this difference varies across sites. The observed difference in ASR and OSR across sites corresponds with higher densities of females (and more female aggression) in northern sites, and higher male densities (and more male aggression) in southern sites (Gerber unpublished). Factors contributing to these differences may include sex-specific responses to distinct levels of anthropogenic stress, variable environmental conditions, and different population trends on each island.

Estimates of λ obtained by including alternate estimates of sex ratio in demographic schedules are shown in Figure 3. As predicted, the 2-sex behavioral-demographic model also provides a more accurate estimate of λ than the 1-sex model. We can also examine how much males matter on particular islands, simply by comparing estimates made from ASR and OSR to the "true" λ obtained by time series methods. As with the estimated sex ratios, estimates of λ based on behavioral–demographic models loosely correlate with latitude. Both the 1-sex and 2-sex models yielded potentially over-optimistic estimates of λ, but slightly lower values were obtained by including sex-specific survival as compared to the single sex model. Including behavioral information with sex ratio yields estimates of λ that more closely match independent estimates from census data. In particular, estimates for each site fall within the 95% confidence interval (CI) for independent estimates of λ from census data. More importantly, estimates of λ, assuming ASR and OSR, bracket the value obtained from census data for each site. In some

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cases, the value obtained assuming ASR is closer to the census data estimate than that from OSR. This suggests that the true breeding sex ratio may be closer to that depicted by ASR than OSR for some sites, and that non-territorial "sneaker" males are contributing to reproductive output differently across sites. These results highlight the potential importance of including behavioral data in population models used for conservation.

Conclusions

Territorial behavior is one mating strategy that probably has strong implications for population viability. Other behaviors (eg conspecific attraction, parental care) may be more or less important in population viability and may be examined within this framework (Panel 1). The intent here is not to provide an exhaustive treatment of the extent to which behavior influences demography, but rather to illustrate an approach for integrating behavioral data into population viability models. Of course, these results should be interpreted with caution, as only one of several alternative hypotheses about the role of behavior in demography is considered. With data for other behavioral hypothesis (eg parental care vs territoriality), λ values obtained from demographic schedules for each island may be compared to independently derived λ values from population trend data (Panel 1).

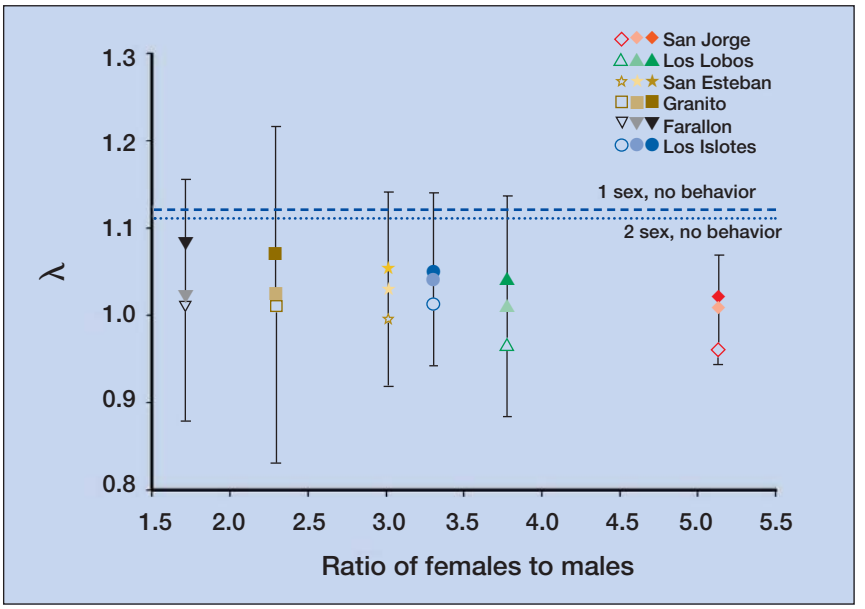

Figure 3. *λ estimate from 2-sex matrix model with fertility function based on actual sex ratio at breeding sites (solid) and behavioral data on operational sex ratio (open). Light shaded symbols are λ values (and bootstrapped 95% CI; Gonzalez-Suarez* et al. *2006) calculated using DA method for empirical estimates based on census data. For comparison, reference lines are shown for single and 2-sex models with no behavior. Alternate demographic schedules may be used in AIC framework to examine putative hypotheses in conjunction with estimates obtained from population trend data.*

Ultimately, the application of this approach is twofold. First, 2-sex behavior-based matrix models can be used to develop a behaviorally-based set of proxies of demographic population viability that could serve as an "early warning system" for conservation practitioners. This approach could potentially circumvent expensive and time-consuming population data collection efforts. For example, if OSR relates positively to population growth rate, low OSR (relative to a previously established baseline level for this parameter) could be used as an index of population health more easily (more sites per year, single year of sampling) than estimation of vital rates (fewer sites, many years of data required).

Second, the approach outlined above could be used to evaluate hypotheses about links between different behaviors and population growth viability (ie λ, or any other metric of population viability). Applying this approach would entail three steps. First, specify a family of behaviors that are hypothesized to be important determinants of vital rates and thus viability (eg maternal attendance, male aggression, or conspecific attraction). Second, develop explicit functions linking these behaviors to vital rates. For example, a female must simultaneously find food and defend her pup, which sets up a conflict between pup growth rate and survival on the rookery. We could therefore ask, "How much foraging is needed for a lactating female to nourish herself and her offspring while minimizing the time away from her pup?" Here, pup survival could be calculated as a function of the increased rewards and risks associated with time spent foraging by females.

Finally, measures of viability (eg λ) may be compared between all candidate models (with different combinations of the behaviors identified as important) to an independent estimate of this parameter, obtained from time series data. Importantly, we can rely on the precision of this independent estimate (ie the 95% CI for the DA estimate of λ) to rule out candidate models. Models with high levels of support would produce λ estimates within the 95% CI for the "true" value from DA methods. Clearly, many candidate models could produce λ values within this range. We can rely on the principle of parsimony and apply Occam's razor, considering the candidate model with the fewest behaviors that falls within the 95% CI of the DA estimate of λ (eg Figure 3). With data for alternate behavioral–demographic models in hand, statistical approaches relying on information theory may help to quantify relative support for these important candidate models (Akaike 1981).

Studies that seek to integrate behavioral data into population studies will advance conservation science by identifying which practical observations of behavioral variation

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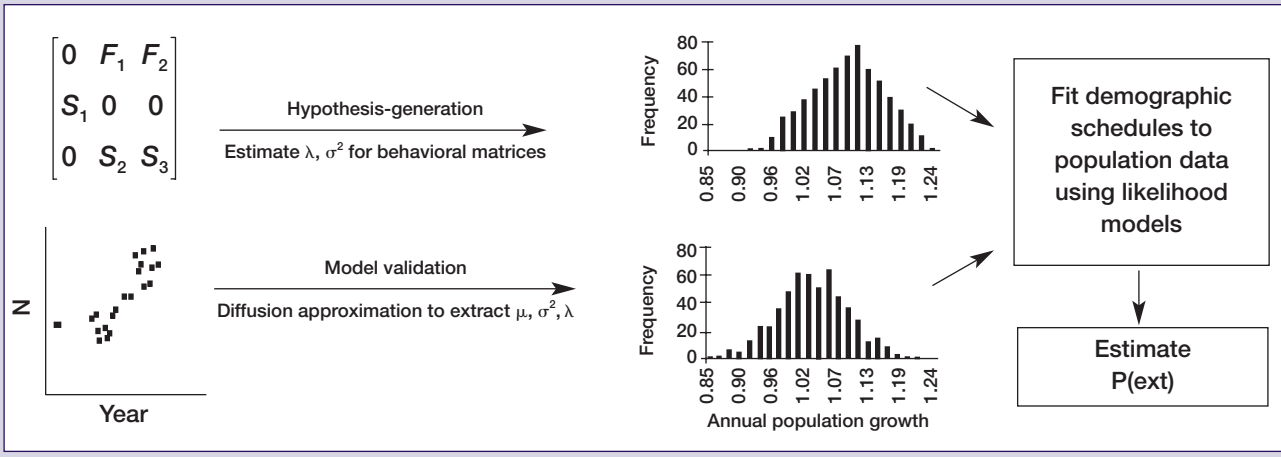
Panel 1. Heuristic framework for using individual based age- and sex-specific behavioral data in population models. With demographic schedules modified by behavior, we may examine the role of behavior on extinction risk. A multi-model inference approach (Burnham and Anderson 1998) may then be taken to evaluate the fit of data predicted by multiple structured population models – in this case, a distribution of population growth rates (λ) – to the same type of data extracted from independently estimated population trend data. Comparison of model fits and selection of best-fit models may be accomplished using Akaike's information criteria to control for variable numbers of parameters in each model (Akaike 1981).



are most important in population models, thereby improving available techniques to estimate extinction risk. A next step will be to apply this approach to determining World Conservation Union (IUCN) and Endangered Species Act risk classification (Gerber *et al.* 1999; Gerber and DeMaster 1999) by incorporating information on behavior into these classification schemes. More generally, this framework may be used to identify the relative effect of alternative management strategies (Beissinger 1997) on population recovery. Using information on animal behavior to design management strategies may only slightly change demographic schedules, but this may be all that is needed to ensure population viability.

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