Contributed Paper

A Behaviorally Explicit Demographic Model Integrating Habitat Selection and Population Dynamics in California Sea Lions

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Abstract: *Although there has been a call for the integration of behavioral ecology and conservation biology, there are few tools currently available to achieve this integration. Explicitly including information about behavioral strategies in population viability analyses may enhance the ability of conservation biologists to understand and estimate patterns of extinction risk. Nevertheless, most behavioral-based PVA approaches require detailed individual-based data that are rarely available for imperiled species. We present a mechanistic approach that incorporates spatial and demographic consequences of behavioral strategies into population models used for conservation. We developed a stage-structured matrix model that includes the costs and benefits of movement associated with 2 habitat-selection strategies (philopatry and direct assessment). Using a life table for California sea lions (*Zalophus californianus*), we explored the sensitivity of model predictions to the inclusion of these behavioral parameters. Including behavioral information dramatically changed predicted population sizes, model dynamics, and the expected distribution of individuals among sites. Estimated population sizes projected in 100 years diverged up to 1 order of magnitude among scenarios that assumed different movement behavior. Scenarios also exhibited different model dynamics that ranged from stable equilibria to cycles or extinction. These results suggest that inclusion of behavioral data in viability models may improve estimates of extinction risk for imperiled species. Our approach provides a simple method for incorporating spatial and demographic consequences of behavioral strategies into population models and may be easily extended to other species and behaviors to understand the mechanisms of population dynamics for imperiled populations.*

Keywords: behavioral ecology, conservation biology, population models, PVA, two-sex demographic models, *Zalophus californianus*

Un Modelo Demográfico Conductualmente Explícito que Integra Selección de Hábitat y Dinámica de Poblaciones de Leones Marinos de California

Resumen: *Aunque ha habido un interés en la integración de la ecología del comportamiento y la biología de la conservación, actualmente se dispone de pocas herramientas para lograr esa integración. La inclusión explícita de información sobre estrategias comportamiento en los análisis de viabilidad poblacional puede incrementar la habilidad de los biólogos de la conservación para entender y estimar los patrones de riesgo de extinción. Sin embargo, los métodos de AVP que consideran comportamiento requieren de datos detallados para individuos que raramente están disponibles para especies en peligro de extinción. Presentamos un método mecanístico que incorpora consecuencias espaciales y demográficas de estrategias de comportamiento en modelos poblacionales utilizados en conservación. Desarrollamos un modelo matricial estructurado en estadios que incluye los costos y beneficios del movimiento asociado con dos estrategias de selección de hábitat (filopatría y evaluación directa). Utilizando una tabla de vida de leones marinos de California (*Zalophus californianus*), exploramos la sensibilidad de las predicciones del modelo a la inclusión de estos parámetros.*

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La inclusión de información conductual dramáticamente cambió los tamaños poblacionales estimados, la dinámica del modelo y la distribución esperada de los individuos entre sitios. Los tamaños poblacionales proyectados a 100 años divergieron hasta en un orden de magnitud entre escenarios que asumían diferente comportamiento. Los escenarios también exhibieron diferentes dinámicas del modelo variando entre equilibrio estable, ciclos y extinción. Estos resultados sugieren que la inclusión de datos de comportamiento en los modelos de viabilidad pueden mejorar las estimaciones del riesgo de extinción de especies en peligro. Nuestro enfoque proporciona un método simple para la incorporación de consecuencias espaciales y demográficas de estrategias de comportamiento en modelos poblacionales y puede ser extendido fácilmente a otras especies y conductas para entender los mecanismos de la dinámica poblacional de especies en peligro de extinción.

Palabras Clave: AVP, biología de la conservación, ecología del comportamiento, modelos demográficos de dos sexos, modelos poblacionales, *Zalophus californianus*

Introduction

Many authors emphasize the need to integrate the fields of behavioral ecology and conservation biology (e.g., Clemmons & Buchholz 1997; Caro 1999; Blumstein & Fernandez-Juricic 2004; Buchholz 2007). Nevertheless, there are few approaches currently available to achieve this integration. For example, population models are likely to be enhanced by explicitly including information about behavioral strategies that affect population dynamics (e.g., Beissinger 1997; Gerber 2006; Rankin & Kokko 2007). Yet behavioral data are rarely incorporated into population viability analyses (PVAs) (but see Ray et al. 1991; Anthony & Blumstein 2000; Gerber 2006) or are incorporated but in complex individual-based models that generally required detailed behavioral information (e.g., Pettifor et al. 2000; Sutherland & Norris 2002; Le Galliard et al. 2005). At the same time, detailed behavioral data are often lacking even for well-studied species. Thus, it is important to develop population models that allow inclusion of key behavioral information for a wide range of species.

The use of simple models that minimize complex model parameterization is practical for both conservation scientists and practitioners. At the same time, the availability of behaviorally explicit models could enhance the use of existing behavioral data in conservation biology. Here, we illustrate an approach to integrate behavioral information into demographic models. Our method allows for consideration of the spatial and demographic consequences of behavior. In particular, expected or estimated costs and benefits of particular behaviors are explicitly included into calculations of demographic parameters (i.e., survival or fertility, see also Greene 2003). We then used these modified parameters in demographic models that considered spatial structure and could be used for population viability analysis. We present an application of this approach that takes into consideration habitat-selection behavior in California sea lions (*Zalophus californianus californianus*).

The California sea lion, a polygynous sexually dimorphic pinniped, represents an interesting study organism for examining questions about habitat selection and demography for several reasons. First, an assessment of this population's viability is urgently needed. The current population status of California sea lion remains unknown, yet some populations (i.e., the Gulf of California, Mexico) have declined by over 20% in the last decade (Szteren et al. 2006). Effective management of California sea lions requires an assessment of their status in light of current threats. Human-induced mortality is still common in the Gulf of California, and sea lion habitat is threatened by coastal destruction, unregulated tourism, and chemical pollution from agriculture and urban areas (Delgado Estrella et al. 1994; Zavala-Gonzalez & Mellink 1997; Brusca et al. 2005). Second, although detailed behavioral data on habitat selection in California sea lions are not currently available, different habitat-selection strategies may occur in this species (Aurioles-Gamboa 1988; Schramm-Urrutia 2002), which can generate very different population dynamics (Belichon et al. 1996). Estimates of viability for this species will be enhanced by an explicit consideration of this behavioral uncertainty.

Habitat selection is the set of mechanisms by which an individual selects the location where it will live and breed. A variety of such mechanisms exist in nature, including philopatry, in which individuals return to their natal patch without gathering any information about the quality of alternative sites (Baker et al. 1995), and direct assessment, in which individuals sample multiple sites and assess quality on the basis of things such as food availability or predation risk (Orians & Wittenberger 1991). These strategies are often different for each sex (Greenwood 1980; Handley & Perrin 2007) and can have different fitness consequences (Doligez et al. 2003). Therefore, variability in these behavioral strategies has the potential to influence population dynamics and spatial structure (Holt 1987). For example, movement among subpopulations is limited in a philopatric species, and this isolation

can reduce population growth and increase risk of extinction (Fahrig & Merriam 1985; Gonzalez-Suarez et al. 2006), affect genetic variability (Mills & Allendorf 1996), and alter patch occupancy (Hill et al. 1996). Direct assessment, on the other hand, may increase mortality of dispersers as a result of increases in predation and spent energy during sampling (Van Vuren & Armitage 1994; Stamps et al. 2005), which could reduce population growth (Amarasekare 1998; Kristan 2003). Philopatry reduces the cost associated with sampling, but individuals may remain in poorer quality habitats, and in smaller populations philopatry may increase the risks of inbreeding depression (Keller & Waller 2002). Direct assessment of habitat, however, allows individuals to explore and presumably select the best quality habitat available; however, individuals must disperse across patches of unsuitable habitat (Stamps et al. 2005). Despite these potentially important effects of site-selection behavior, current population models rarely incorporate information about habitat-selection strategies in their calculations (but see Possingham & Davies 1995; Amarasekare 1998; Greene 2003).

Our primary goal was to devise a simple approach to incorporate habitat-selection behavior in population models typically used for conservation and in doing so address the need for integration in the fields of behavioral ecology and conservation biology. We used data on California sea lions to provide an applied example and to illustrate the importance of explicitly considering behavior when exploring population dynamics.

Methods

Models

Most existing population models only consider the female segment of the population and use single-sex models (Caswell 2001). Nevertheless, habitat-selection behavior in California sea lions is likely to be sex specific (Trujillo et al. 2004; Hoffman et al. 2006). Therefore, we constructed and explored 2 demographic models: single-sex (female-based) and 2-sex matrix. In particular, we developed a stage-structured matrix model that considered spatial dynamics (i.e., movement rates) and expected costs (i.e., cost for the animal to move and cost to remain at a site) of 2 breeding-site selection strategies exhibited by California sea lions: philopatry and direct assessment (Table 1). Our model depicts a California sea lion life cycle with 3 life stages and discrete breeding seasons. We based life stages on categories commonly used during population counts: pups (individuals from 0 to 1 year old), juveniles (individuals from 1 to 4 years old), and adults (individuals older than 4 years old; Aurioles-Gamboa & Zavala-Gonzalez 1994). Vital rates for each stage were calculated from age-specific survival data for California sea lions from Los Islotes Island in the Gulf of California (Hernández-Camacho 2001; Gerber 2006). We used the approach described by Ebert (1999) to convert these age-specific survival rates to stage-based rates. In particular, we converted survival rates by calculating the overall stage rate, s_s ($s_{x+\Delta x}/s_x$, where s_x are the age-specific survival rates), and then using s_s to compute the annual rate ($\sqrt[n]{s_s}$, where n is the number of years included in that stage). We multiplied the annual rate by the proportion remaining in the stage class (1-1/number of years in stage) to obtain the stage survival rates (s and S in Table 2). Growth rates were calculated by multiplying the annual survival rate by the proportion leaving the stage (1/number of years in stage, g and G in Table 2).

Empirical estimates of fertility rates are currently not available for male and female California sea lions (but see Hernández-Camacho et al. 2008); thus, we used the harmonic mean birth function adjusted for polygynous mating systems (Caswell 2001):

$$F_f = \frac{k \cdot A_m^t}{\left(A_m^t + A_f^t \cdot h^{-1}\right)}. \quad (1)$$

This function accounts for the abundance of both sexes at each time step (A_m^t is abundance of adult males and A_f^t of adult females), the litter size (k, which in sea lions equals 1, Riedman 1990), and the harem size (h, which we estimated as equal to 6 on the basis of 4 years of behavioral observation data from Los Islotes Island (L.R.G., unpublished data). Because males were not considered in the single-sex model, a single, fixed female-fecundity value was calculated from Eq. 1, with initial abundance

Table 1. Assumed costs, benefits, and spatial consequences of 2 site-selection strategies of California sea lions.

Strategy	*Benefits*	*Costs*	*Spatial consequences*
Direct assessment	higher fecundity when best quality site is selected	sampling cost (d) reduce survival	movement between sites
Philopatry	no sampling cost	lower fecundity if remaining at low-quality site	no movement (remain at natal site)

Table 2. Variables and parameters used in the proposed behaviorally explicit model for California sea lions.[a]

Parameters and variables	*Description*	*Values (range) or equations*
P^t_{fa}	number of female pups (individuals from 0–1 year old) in site a at time t (P^t_{ma} for males; and P^t_{fb} or P^t_{mb} for site b)	Eq. 2
J^t_{fa}	number of juvenile females (individuals from 1–4 year old) in site a at time t (J^t_{ma} for males; and J^t_{fb} or J^t_{mb} for site b)	Eq. 2
A^t_{fa}	number of adult females (individuals older than 4 years old) in site a at time t (A^t_{ma} for males; and A^t_{fb} or A^t_{mb} for site b)	Eq. 2
N^t_a	total population size in site a at time t (N^t_b for site b)	$N^t_a = P^t_{fa} + J^t_{fa} + A^t_{fa} + P^t_{ma} + J^t_{ma} + A^t_{ma}$
s	survival rate of juveniles	$s_f = 0.6636^b$ $s_m = 0.6486^b$
S	survival rate of adults	$S_f = 0.9764^b$ $S_m = 0.8812^b$
g	growth rate of pups to juveniles	$g_f = 0.7979^b$ $g_m = 0.6146^b$
G	growth rate of juveniles to adults	$G_f = 0.2212^b$ $G_m = 0.2162^b$
F_f	basic fertility rate: number of female pups born from an adult female per year (F_m for males)	Eq. 1
I^t_a	discount factor that represents the density-dependent cost of staying (i.e., reduction in survival) at site a at time t (I^t_b for site b)	Eq. 3
δ	parameter that determines the strength of the relationship between I and N/K	0.5; 5
K_a	resource abundance or carrying capacity of site a (K_b for site b)	424; 500
d	sampling costs associated with movement; reduction in survival for those individuals that move	[0, 1]
m^t_{fab}	proportion of adult females that use direct assessment and move from breeding site a to site b at time t (m^t_{fba} for site b to a; m^t_{mab} and m^t_{mba} for males)	Eq. 4
m_{fo}	proportion of females that use direct assessment as a strategy (e.g., $m_{fo} = 0$ is an all-philopatric population, whereas $m_o = 1$ is an all-assessor population; [m_{mo} for males])	[0, 1]

[a] *Subscript* f *indicates female portion of the population, and subscript* m *indicates male portion.*
[b] *Calculated from Hernández-Camacho (2001).*

data as a basis for comparison with the 2-sex fecundity function.

The calculated stage-specific vital rates were included in a single-sex or a 2-sex demographic matrix that describes 2 discrete breeding sites (a and b) between which individuals may move (Eq. 2). Equation 2 displays the 2 population vectors (population at time t and at time $t + 1$) and the 2-sex transition matrix. We constructed the single-sex model by reducing all male-associated functions and variables to 0 in Eq. 2.

$$\begin{pmatrix} P^{t+1}_{fa} \\ J^{t+1}_{fa} \\ A^{t+1}_{fa} \\ P^{t+1}_{ma} \\ J^{t+1}_{ma} \\ A^{t+1}_{ma} \\ P^{t+1}_{fb} \\ J^{t+1}_{fb} \\ A^{t+1}_{fb} \\ P^{t+1}_{mb} \\ J^{t+1}_{mb} \\ A^{t+1}_{mb} \end{pmatrix} = \left(\begin{array}{ccc:ccc:ccc:ccc} 0 & 0 & f_f \cdot I^t_a & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ g_f & s_f & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & G_f & (1-m^t_{fab}) \cdot S_f & 0 & 0 & 0 & 0 & 0 & (1-d_f) \cdot S_f \cdot m^t_{fba} & 0 & 0 & 0 \\ \hdashline 0 & 0 & 0 & 0 & 0 & f_m \cdot I^t_a & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & g_m & s_m & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & G_m & (1-m^t_{mab}) \cdot S_m & 0 & 0 & 0 & 0 & 0 & (1-d_m) \cdot S_m \cdot m^t_{mba} \\ \hdashline 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & f_f \cdot I^t_b & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & g_f & s_f & 0 & 0 & 0 & 0 \\ 0 & 0 & (1-d_f) \cdot S_f \cdot m^t_{fab} & 0 & 0 & 0 & 0 & G_f & (1-m^t_{fba}) \cdot S_f & 0 & 0 & 0 \\ \hdashline 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & f_m \cdot I^t_b \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & g_m & s_m & 0 \\ 0 & 0 & 0 & 0 & 0 & (1-d_m) \cdot S_m \cdot m^t_{mab} & 0 & 0 & 0 & 0 & G_m & (1-m^t_{mba}) \cdot S_m \end{array}\right) \times \begin{pmatrix} P^t_{fa} \\ J^t_{fa} \\ A^t_{fa} \\ P^t_{ma} \\ J^t_{ma} \\ A^t_{ma} \\ P^t_{fb} \\ J^t_{fb} \\ A^t_{fb} \\ P^t_{mb} \\ J^t_{mb} \\ A^t_{mb} \end{pmatrix} \quad (2)$$

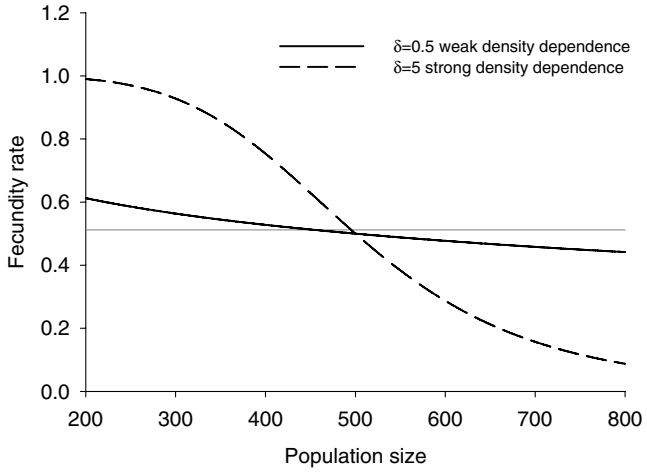

*Figure 1. Relationship between population size and fecundity rate for 2 levels of density-dependence regulation (parameter δ in Eq. 2). Gray line is the baseline fecundity (*F*) from Table 2 (*K = 500*).*

Additional descriptions and values for the parameters and variables used in Eq. 2 are given in Table 2. In the transition matrix, the top half of the matrix describes the dynamics of females and males at site a (left section) and the movement of adults from site b to site a (right section). The bottom half of the matrix describes the dynamics of females and males at site b (right section) and the movement of adults from site a to site b (left section). For consistency, we used the abundance estimate for Los Islotes Island in 2004 as the starting population size for both sites in all scenarios (L.R.G., unpublished data). Nevertheless, estimated population sizes at equilibrium were independent of initial population size.

Our demographic matrix explicitly incorporated the assumed costs of philopatry and direct assessment (Table 1). In particular, the cost of staying at a given site was represented by I (Eq. 3), a discount factor modeled as a density-dependent function that affected the basic fertility rate (from Dobson & Lyles 1989):

$$I_a^t = \frac{1}{\left(1 + (N_a^t / K_a)^{\delta}\right)}. \qquad (3)$$

Descriptions and values for the parameters and variables in Eq. 3 are in Table 2. The cost of staying increased as populations approached the site's carrying capacity (K); thus, the actual fertility rate ($f \cdot I$) decreased as populations increased. Figure 1 illustrates this for the 2 values of δ we explored (δ = 0.5, weak density dependence: smaller effect of population size on fertility; and δ = 5, strong density dependence: larger effect of population size on fertility). For simplicity, we assumed males and females experienced the same cost of staying (i.e., both affected similarly by density).

Our model also included a cost associated with moving, represented by d_f (or d_m), that affected the survival rate of dispersing individuals. This cost was allowed to vary between 0 and 1, where $d = 0$ represented no cost of moving and $d = 1$ resulted in 100% mortality of those individual moving. In some scenarios, the value of d differed for females and males to reflect sex biases in dispersal behavior or in risks associated with moving.

Movement dynamics were incorporated with m_{fab}^t (Eq. 4), which represents the proportion of adult females that use direct assessment and thus, move from breeding site a to site b at time t. The expression m_{fba}^t represents movement from site b to a at time t, and in the same way, m_{mba}^t and m_{mab}^t represent adult male movement. In classical habitat-selection models (Fretwell & Lucas 1970), individuals have perfect knowledge of site quality and move accordingly. In reality, however, animals rarely have such knowledge (e.g., Battin 2004). Therefore, we used a quality-dependent movement rule in which assessors generally moved to the higher-quality sites but occasionally chose a lower-quality location in error. This approach assumes that even when sites are equal in quality some individuals using direct assessment may still move because individuals may not always be able to discriminate among sites of very similar or identical quality. In

$$m_{\text{fab}}^t = m_{\text{fo}} \cdot \left(1 - \frac{I_a^t}{I_a^t + I_b^t}\right), \qquad (4)$$

the proportion of individuals using direct assessment as a behavioral strategy is represented by m_o (m_{fo} for females and m_{mo} for males). For example, $m_{\text{fo}} = 0$ represents a population in which all females are philopatric, whereas $m_{\text{fo}} = 1$ represents a population in which all females are assessors. Subsequently, m_{fab}^t reflects those female assessors who actually move on the basis of site quality differences at time t. Site quality was represented by the difference in fertility rates between sites at time t because fertility may be considered a proxy for habitat quality (Switzer 1997). In our model the value of I (Eq. 2) determined the actual fecundity rate. This approach incorporates some behavioral plasticity by considering that assessor behavior (i.e., the decision to move or stay) is flexible and density dependent. Nevertheless, individual behavioral strategies (philopatry and direct assessment) are assumed to be fixed, so each individual is either philopatric or an assessor.

Sensitivity Analysis

We explored the dynamics of both versions of the model (2-sex and single-sex) considering weak (δ = 0.5) and strong (δ = 5) density dependence in a heterogeneous habitat (quality differed among sites such that $K_a = 500$ and $K_b = 424$ for the 2-sex version and $K_a = 350$ or $K_b = 279$ for the single-sex version). In the high-quality habitat scenarios ($K = 500$ or 350), the simulation was initiated

at the carrying capacity (i.e., all site resources were already being exploited). The K values for these scenarios were chosen on the basis of maximum corrected census count at Los Islotes Island (L.R.G., unpublished data, corrected as in Szteren et al. 2006), which can be considered as the carrying capacity of that site. For the low-quality ($K = 424$ or 279) scenarios, we assumed that at $t = 0$, some site resources are still unexploited. Using these values of δ and K, we numerically determined which values of m_{fo} and m_{mo} (proportion of assessors in the population) and d_f and d_m (sampling costs) resulted in the following stable states of the population: stable equilibria ($N > 0$), extinction ($N = 0$), or oscillatory dynamics (cycles).

In addition, we used the 2-sex model to explore how different habitat-selection strategies and costs affected sea lion population trajectories projected over 100 years. Currently, the habitat selection behavior of California sea lions remains unknown; therefore, we explored 3 plausible behavioral scenarios: a population of mostly philopatric individuals ($m_{fo} = m_{mo} = 0.1$), a population of mostly assessors ($m_{fo} = m_{mo} = 0.9$), and a population of mostly philopatric females and mostly assessor males (male-assessor population: $m_{fo} = 0.1$ $m_{mo} = 0.9$), which is typical of polygynous mammals (Greenwood 1980). For each scenario we also considered a range of sampling costs: no cost for all individuals ($d_f = d_m = 0$), low cost for all individuals ($d_f = d_m = 0.1$, which represents a 10% reduction in survival for those assessing), high cost for all individuals ($d_f = d_m = 0.3$, 30% reduction in survival), and low costs for females but high costs for males ($d_f = 0.1$ $d_m = 0.3$). These costs reflect a range of empirical sampling costs found in studies of other species because no data are currently available for sea lions (Van Vuren & Armitage 1994; Alberts & Altmann 1995; Baker & Rao 2004; Schtickzelle et al. 2005). We also explored the 2 density-dependent relationships described earlier ($\delta = 0.5$ and $\delta = 5$). Results are presented as site population trajectories over 100 years.

Results

Comparing Single- and 2-Sex Population Models

Patterns of extinction were considerably different between the single- and 2-sex models, with populations becoming extinct under a wider range of conditions in the single-sex model (Fig. 2). For the single-sex model, populations with as few as 58% assessors became extinct when sampling costs were highest ($d = 1$), whereas the same sampling costs only caused extinction in populations with >87% assessors in the 2-sex model (Fig. 2). In both models extinction dynamics were not noticeably influenced by the strength of the density dependence considered. Oscillatory dynamics (cycles) only occurred under scenarios that assumed strong density dependence ($\delta = 5$) and arose under similar behavioral conditions for both model versions. Cycles occurred in populations with >21% assessors exposed to low to medium sampling costs ($d < 0.50$ for the 2-sex model and $d < 0.43$ for the single-sex model).

Sensitivity Analysis: Model Dynamics When Behavior Is Sex Specific

When behavior differed between sexes, population cycles were limited to scenarios that assumed strong density dependence ($\delta = 5$), but extinction patterns were similar for both values of δ. Exploring sex-specific behavioral patterns revealed that population dynamics were mostly driven by female behavior (Fig. 3). For example, populations with <80% female assessors never became extinct, whereas populations with no male assessors became extinct under certain conditions (i.e., >96% female assessors and very high sampling costs). Moreover, extinction did not occur unless females were exposed to high sampling costs, whereas the magnitude of the male sampling costs had only a small effect on extinction risk (Fig. 3). The importance of females was also illustrated in the oscillatory behavior patterns. Cycles did not occur in populations with <20% female assessors, but arose under all ranges of male behavior (Fig. 3). Nevertheless, male behavior was not irrelevant: risk of extinction and tendency to cycle were higher when the proportion of male assessors in the population was greater (Fig. 3).

Sensitivity Analysis: Population Trajectories

Assuming individuals in a population have different habitat selection strategies, even without changing other parameters in the model, resulted in differences of up to 1 order of magnitude in estimated population size projected over 100 years (compare lines within each panel in Fig. 4). In general, mostly philopatric populations (described in Methods) had the largest population sizes because only a few individuals in these populations experienced sampling costs, whereas mostly assessor populations often had the smallest population sizes. Nevertheless, these general results were affected by the sampling costs and the strength of density dependence assumed. In scenarios that assumed weak density dependence, the difference in size among populations was greater when sampling costs were largest (compare Fig. 4a with Fig. 4e). In contrast, in scenarios that assumed strong density dependence, differences were greater when sampling costs were lowest. This reverse trend was the result of oscillatory behavior in mostly assessor populations. Fluctuations in size were more marked in these populations when sampling costs were zero or low (Figs. 4b and 4d) and resulted in periodic large differences in population sizes and overall larger mean sizes for populations with more assessors.

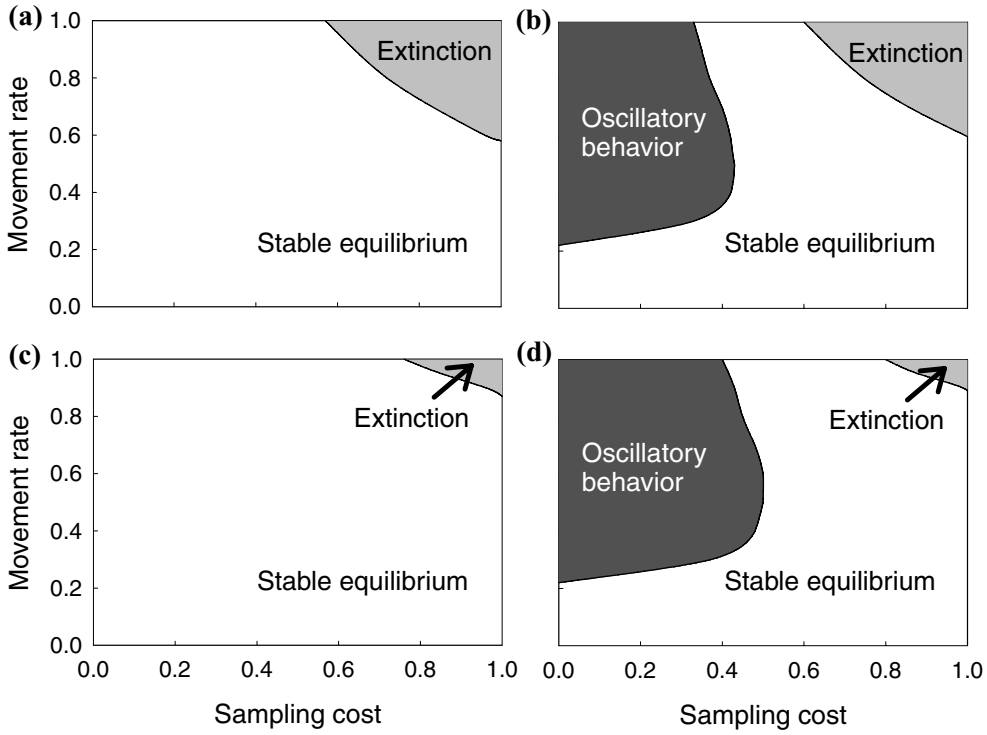

Figure 2. Dynamic behavior of a population model for California sea lions in which different stable states are reached depending on the proportion of assessors (m_o, i.e., individuals that use direct assessment as a habitat selection mechanism) in that population and the sampling costs (d, reduction in survival for those individuals that move) they pay: (a) single-sex model under a scenario with weak density dependence ($\delta = 0.5$), (b) single-sex model under a scenario with strong density dependence ($\delta = 5$), (c) 2-sex model under a scenario with weak density dependence ($\delta = 0.5$), and (d) 2-sex model under a scenario with strong density dependence ($\delta = 5$). In the 2-sex version, the proportion of female assessors is equal to the proportion of male assessors and both sexes are exposed to the same sampling costs.

In addition, heterogeneity of the habitat affected philopatric and assessor populations differently. In general, as predicted by models such as the "ideal free distribution" (Fretwell & Lucas 1970), populations in higher-quality sites (N_a, $K_a = 500$) were generally larger than those in lower-quality habitats (N_b, $K_b = 424$, Fig. 4). Nevertheless, the magnitude of the difference depended on the behavioral strategy that dominated the population. Populations of mostly assessor or male-assessor populations were generally more evenly distributed between sites than were mostly philopatric populations (Fig. 4). At times, however, cyclic fluctuations in mostly assessor populations created large differences between low- and high-quality sites and even resulted in low-quality site populations being temporarily larger than those in higher-quality sites.

Discussion

Including Habitat-Selection Behavior in Demographic Models

We propose a mechanistic approach to incorporate behavioral information into population models that takes into account changes in spatial dynamics (i.e., movement rates) and vital rates (i.e., added costs) expected from different mechanisms of site selection. In our modeled scenarios for California sea lions, inclusion of these behavioral data significantly affected predicted population dynamics, projected population sizes, site occupancy, and distribution patterns. For example, model behavior changed from stable equilibrium to extinction (or oscillatory behavior), depending on the assumed proportion of assessors and sampling costs in the population (Figs. 2 & 3). As expected, very high sampling costs in populations with many assessors often led to extinction. Nevertheless, under certain conditions (i.e., strong density dependence, Fig. 2), sampling costs stabilized dynamics illustrating a potential benefit of such costs. Stable dynamics may reduce the probability of extinction in a stochastic environment because fluctuating populations become more vulnerable to environmental catastrophes during periods of low population size (see also Amarasekare 1998).

In addition, we found projected population sizes differed considerably between scenarios (Fig. 4). In most cases, mostly philopatric populations had the highest

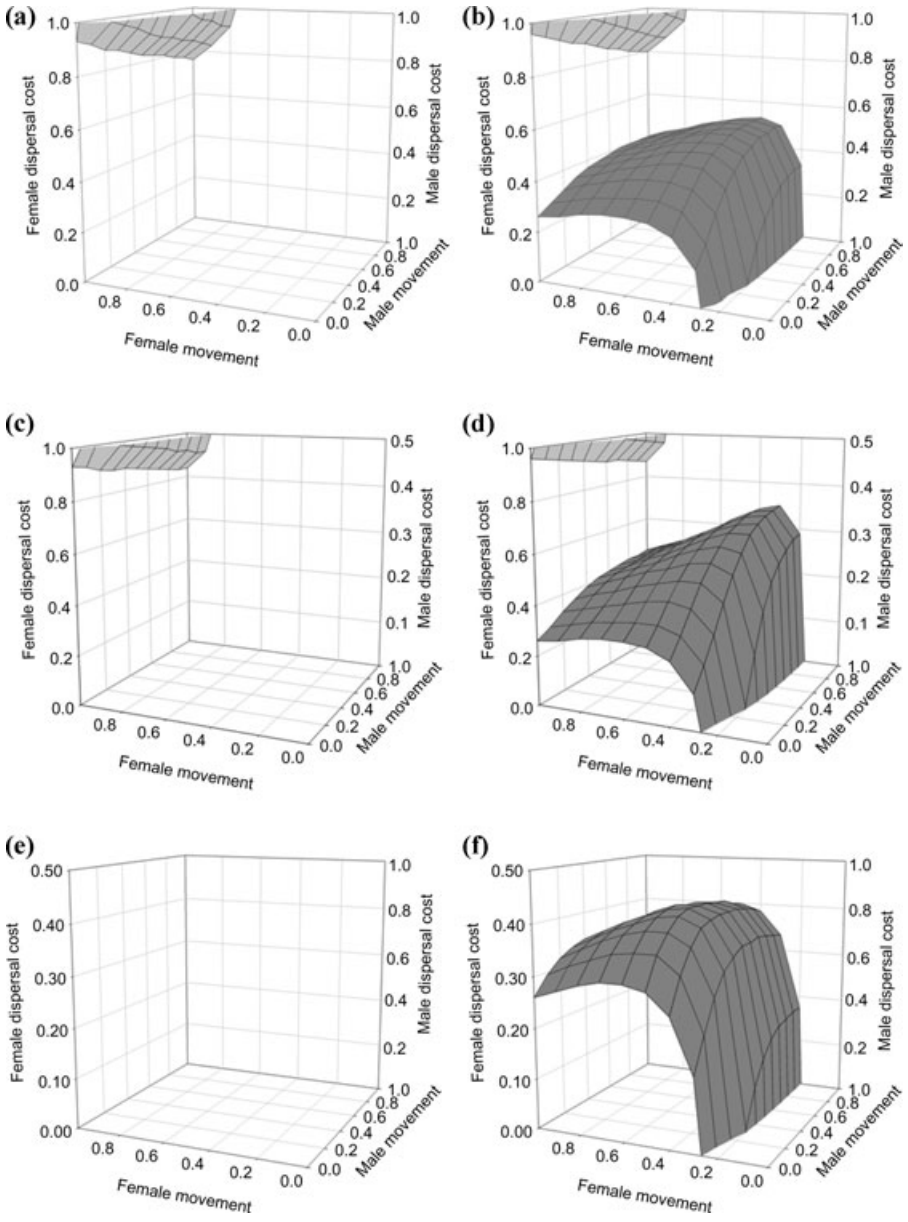

Figure 3. Dynamic behavior of a 2-sex population model for California sea lions in which different stable states are reached depending on the proportion of female and male assessors (m_{fo} and m_{mo}) in that population and the sampling costs each sex pays (d_f and d_m) (dark gray, oscillatory dynamics; light gray, extinction [$N<0$]; white, stable population [$N>0$]): (a) weak density dependence ($\delta = 0.5$) and equal sampling costs for male and female assessors, (b) strong density dependence ($\delta = 5$) and equal sampling costs for male and female assessors, (c) weak density dependence ($\delta = 0.5$) and female assessors paying half the sampling costs of males ($d_f = 0.5 \cdot d_m$), (d) strong density dependence ($\delta = 5$) and female assessors paying half the sampling costs of males ($d_f = 0.5 \cdot d_m$), (e) weak density dependence ($\delta = 0.5$) and male assessors paying half the sampling costs of females ($d_m = 0.5 \cdot d_f$) (all explored scenarios resulted in stable population sizes > 0), and (f) strong density dependence ($\delta = 5$) and male assessors paying half the sampling costs of females ($d_m = 0.5 \cdot d_f$).

population sizes (see also Holt 1985) because only a few individuals experienced sampling costs. Nevertheless, when the costs of staying were high (strong density dependence), populations with a higher proportion of assessors, even those exposed to some sampling costs, had larger predicted population sizes than philopatric groups (Fig. 4). As expected, mostly assessor populations experiencing high sampling cost generally had the lowest projected sizes, although no extinctions were predicted within the range of realistic costs explored for this species. Including behavioral information also changed predicted site occupancy and distribution patterns. The distribution of individuals between low- and high-quality sites was influenced by the behavioral strategy assumed for the population. Mostly philopatric populations generally exhibited the larger differences among sites, whereas mostly assessor populations were often similar in size among sites of different quality (Fig. 4). Under some conditions, however, oscillatory dynamics in mostly assessor groups caused large fluctuations in the number of individuals occupying high-quality versus low-quality sites.

Our results indicate inclusion of habitat-selection behavior in population models considerably affects population viability predictions. Nevertheless, there are several caveats to the application of our approach to California sea lion data. First, we used a simplification of a life cycle and explored a limited range of scenarios and behaviors to illustrate the proposed approach. For example, our model simplifies behavioral complexity by considering only 2 behavioral strategies (i.e., individuals are either philopatric or assessors). In reality, individuals may have varying tendencies to disperse, with some animals being

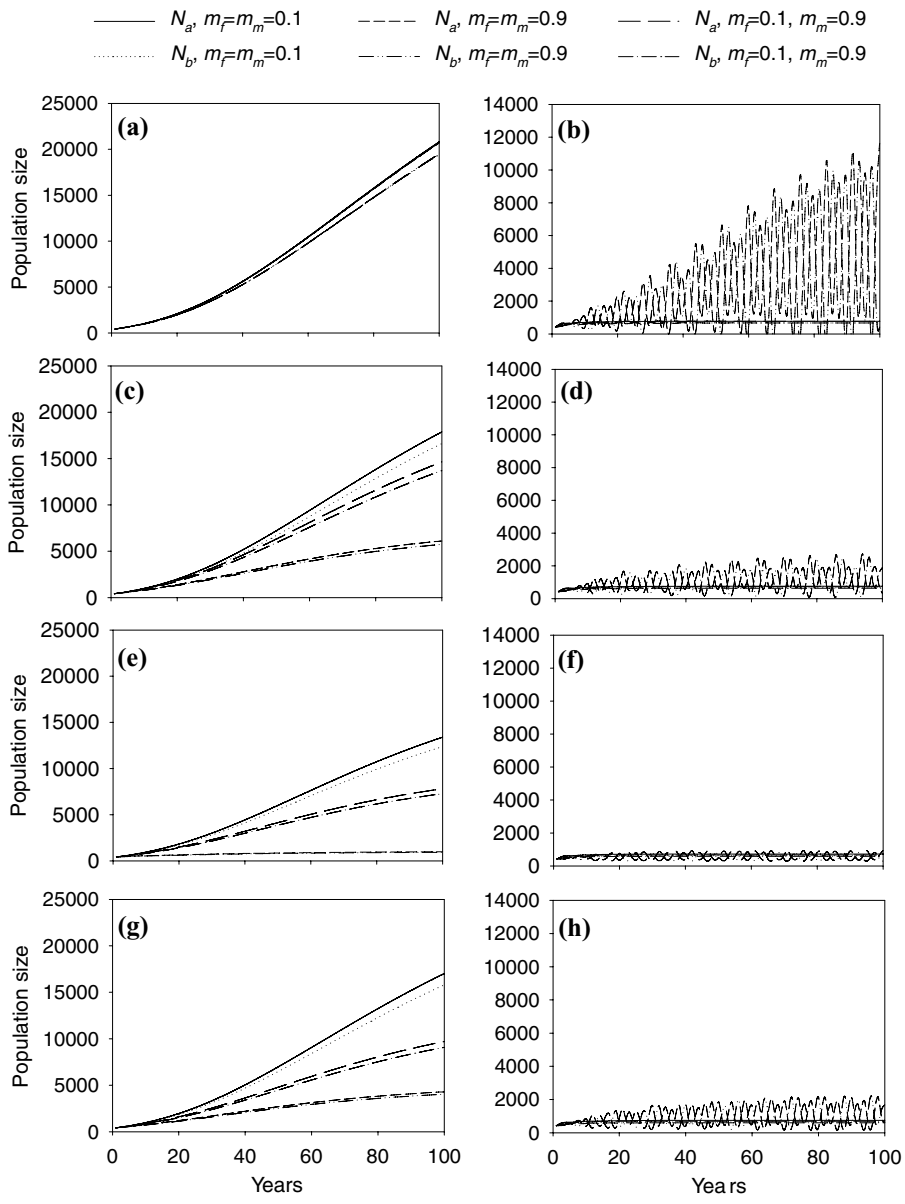

Figure 4. Site population trajectories over 100 years in heterogeneous habitats (K_a = 500, K_b = 424) for different combinations of parameter values in the 2-sex model (see Sensitivity Analysis in Methods): (a) weak density dependence (δ = 0.5) and no dispersal costs for either sex ($d_f = d_m = 0$), (b) strong density dependence (δ = 5) and no dispersal costs for either sex ($d_f = d_m = 0$), (c) weak density dependence (δ = 0.5) and low dispersal costs for either sex ($d_f = d_m = 0.1$), (d) strong density dependence (δ = 5) and low dispersal costs for either sex ($d_f = d_m = 0.1$), (e) weak density dependence (δ = 0.5) and high dispersal costs for either sex ($d_f = d_m = 0.3$), (f) strong density dependence (δ = 5) and high dispersal costs for either sex ($d_f = d_m = 0.3$), (g) weak density dependence (δ = 0.5) and low dispersal costs for females ($d_f = 0.1$) and high for males ($d_m = 0.3$), and (h) strong density dependence (δ = 5) and low dispersal costs for females ($d_f = 0.1$) and high for males ($d_m = 0.3$). In panels (a) and (b), multiple trajectories overlap.

more dispersal-prone than others. We also ignored alternative mechanisms of site selection, such as conspecific attraction (Stamps 1988), and additional costs, such as inbreeding depression in small populations of philopatric individuals (Keller & Waller 2002). Another potential caveat is the way in which we modeled direct assessment. We based site selection on fecundity rates and allowed some sampling error, and this may not be adequate or applicable in all situations. Nonetheless, because our goal was to illustrate an approach to integrate behavioral data into population models, and not to characterize all aspects of behavioral complexity or accurately determine California sea lion viability, we believe these simplifications were justified. We expect that our approach could be generalized to other species and other behaviors in which additional information may be available and could be used to obtain a more accurate estimate of California sea lion viability as behavioral data on habitat selection become available. In particular, although we used a deterministic model for simplicity, we expect this approach could be applied to more realistic stochastic and complex age-structure models.

Need for 2-Sex Models

Population models are often derived from the female segment of the population and male presence is ignored; however, our results suggest including males can affect predictions about population extinction risk (see also Rankin & Kokko 2007). Even though in our case population dynamics were mostly driven by female behavior, male behavior influenced the results, suggesting male dynamics and behavior should be explicitly considered. For example, extinctions happened under a wider range of

conditions in the single-sex model. Although the particular effects of including male data are likely to depend on the biology of the species, our results highlight the importance of including both male and female data in population models used for conservation.

The Future of Behavioral-Demographic Models

We have proposed a simple approach to incorporate behavioral information on habitat selection into population models. This general approach could be applied to other behaviors, species, and population models by applying the following 5 steps:

1. Identify relevant behaviors likely to affect population dynamics in the studied species.
2. Empirically measure the spatial and demographic (i.e., costs and benefits) consequences of these behaviors. If obtaining these empirical data is not possible, this approach could still be applied by exploring scenarios determined on the basis of educated guesses.
3. Incorporate empirical behavioral data (or educated guesses) into a matrix population model by altering vital rates and explicitly representing spatial dynamics.
4. Estimate population viability with these modified models.
5. Explore sensitivity of the predictions to the inclusion of behavioral data.

Applying this approach to California sea lion data, we found that predictions of population viability that do not consider behavior may lead to biased estimates of extinction risk, even in situations in which habitat quality and vital rates are fairly well understood. Recognizing that behavioral data are not always available for imperiled species (Macdonald & Johnson 2001) and may be difficult to obtain (Baguette et al. 2000), our results indicate that ignoring behavior may lead to erroneous estimates of viability. Therefore, our approach incorporates behavioral information into simple population models, circumventing the need to use complex representations that often require data for a large number of parameters. Extrapolating model parameters from similar species may lead to questionable viability predictions, even when parameters are generalized from populations of the same species (Mennechez et al. 2004). Therefore, when data are limited, it is important to use approaches that minimize the number of parameters to be estimated while making the best use of available data. In other words, although conservation efforts might be ineffective when behavioral subtleties are ignored, including too much detail in viability models may reduce our capacity to understand true dynamics and make rational conservation decisions.

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