Developing Behavioral Indices of Population Viability:

A Case Study of California Sea Lions

in the Gulf of California, Mexico

by

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ABSTRACT

Despite years of effort, the field of conservation biology still struggles to incorporate theories of animal behavior. I introduce in Chapter I the issues surrounding the disconnect between behavioral ecology and conservation biology, and propose the use of behavioral knowledge in population viability analysis. In Chapter II, I develop a framework that uses three strategies for incorporating behavior into demographic models, outline the costs of each strategy through decision analysis, and build on previous work in behavioral ecology and demography. First, relevant behavioral mechanisms should be included in demographic models used for conservation decision-making. Second, I propose rapid behavioral assessment as a useful tool to approximate demographic rates through regression of demographic phenomena on observations of related behaviors. This technique provides behaviorally estimated parameters that may be applied to population viability analysis for use in management. Finally, behavioral indices can be used as warning signs of population decline. The proposed framework combines each strategy through decision analysis to provide quantitative rules that determine when incorporating aspects of conservation behavior may be beneficial to management. Chapter III applies this technique to estimate birthrate in a colony of California sea lions in the Gulf of California, Mexico. This study includes a cost analysis of the behavioral and traditional parameter estimation techniques. I then provide in Chapter IV practical recommendations for applying this framework to management programs along with general guidelines for the development of rapid behavioral assessment.

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I dedicate this work to my family

for nurturing my love of nature.

ACKNOWLEDGMENTS

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I. INTRODUCTION

The Cost of Conservation

A significant portion of the limitations of biological conservation stems

from the cost of preserving habitats, monitoring populations, and enforcing

management decisions (Moore *et al.* 2004; Naidoo *et al.* 2006). Often

conservation biologists and wildlife managers must divide limited funds between

these and other conservation objectives. This limits the amount of resources

government agencies and non-profit organizations are able to invest to increase

their understanding of the biology of managed populations and the various threats

affecting them. One important method of collecting these data is to establish

regular monitoring programs of these populations to collect data on abundance,

reproduction and mortality rates, and the number and magnitude of direct and

indirect human interactions (Beissinger and McCullough 2002; Morris and Doak

2002; Nichols and Williams 2006). These monitoring programs provide baseline

data that can be used for making management and policy decisions, including

determining if the populations are threatened with decline (Beissinger and

Westphal 1998; Morris *et al.* 2002). More recently, emphasis has been placed on

monitoring protected populations to quantify the effects of management decisions,

which influence the establishment of future policies and preserves (Kapos *et al.*

2008). These monitoring programs, however, often involve costly, time-intensive

techniques to obtain informative estimates of demographic rates (Sandercock

2006). This time lag between data collection and decision-making can mean life

or death in threatened populations. The need for informative data gathered in a

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short period of time has resulted in the use of techniques to rapidly assess the status of threatened populations and environmental variables associated with their declines (e.g., Rapid Ecological Assessment - The Nature Conservancy; Rapid Assessment Program - Conservation International; Oliver and Beattie 1993; O'Dea *et al.* 2004).

The Benefit of Behavior?

Beginning in the mid-1990's, many behavioral ecologists started to advocate the use of theories of behavioral ecology in the conservation of animal species (Anholt 1997; Caro 1998; 1999; Anthony and Blumstein 2000; Gosling and Sutherland 2000; Festa-Bianchet and Apollonio 2003; Blumstein and Fernández-Juricic 2010). Many of the works they produced with conservation in mind detailed specific programs where behavior was suspected to be a benefit or had been considered over the course of the management program. The main argument of these studies was that including information on a particular animal's behavior resulted in better management outcomes (i.e., higher productivity in captive breeding programs, more effective preserve designs, etc.; Caro 1998). This field eventually came to be known as conservation behavior (Buchholz 2007).

However, despite advances in particular management programs, Caro (2007) conceded that theories of behavioral ecology may not be applicable to as wide a range of conservation issues as was first thought. He pointed to the mismatch between the theories and the conservation problems as the main reason

for this limited application. He argued that knowledge of particular behaviors can benefit conservationists, but we must focus on the conservation problems before trying to apply behavioral theories. Unfortunately, this focus on the case studies of where behavior can improve and has contributed to conservation programs has led to a disorganized grouping of conservation behavior ideas, some with applied examples, but no intuitive way to consider behavior in management (Linklater 2004; Angeloni *et al.* 2008).

To ameliorate this problem, Berger-Tal *et al*. (2011) attempted to attack this amalgamation of uncoordinated examples with their framework for conservation behavior. They divided their framework into three conservation themes stemming from behavioral phenomena: 1) Anthropogenic impacts on animal behavior; 2) Behavioral indicators; and 3) Behavior-based management. This framework serves to group the examples of previous conservation behavior successes into general categories, yet does not provide wildlife managers with an accessible method of applying this behavioral knowledge to conservation issues.

Research Approach and Objectives

The conceptual framework outlined in this work approaches conservation behavior from a different angle. Instead of working from the behavioral ecologist perspective, I take Caro's advice and focus on a specific conservation problem: the need for increased wildlife monitoring and data collection while balancing program costs. This problem arises from the increasing use of demographic models of population dynamics in management and policy (Beissinger and

Westphal 1998; Morris *et al.* 2002; Gerber and Heppell 2004). These models are used to perform a population viability analysis on the managed species to aid policy makers and wildlife managers in evaluating the impacts of their decisions on the population of concern by providing quantitative measures of the population's probability of future decline (Lindenmayer *et al.* 1993; Drechsler and Burgman 2004). The wide use of these models in conservation programs and policy make them a practical candidate for a broad application to conservation behavior.

      The following conceptual framework incorporates behavioral knowledge into demographic models 1) when these behaviors increase the predictive ability of demographic models of monitored populations; and 2) as indicators of population dynamics. Furthermore, I propose a possibly useful technique to implement point (2) that approximates demographic parameters through correlation with behavioral indicators. The latter strategy has the potential to provide managers with rapid assessments of vital population information while reducing the costs of monitoring the population. This framework fits into that of Berger-Tal *et al.* (2011) through their themes of behavioral indicators and behavior-based management, but includes a more applied perspective than this previous work. I address the costs and benefits of each strategy by placing them in a decision analysis, which provides practical rules of when animal behaviors should be included in the monitoring and modeling process. Chapter II outlines this applied framework, building from examples of previous studies of animal

behavior and demography, with the emphasis on reproductive, foraging, and anti-predator behaviors.

Chapter III provides an applied example of the use of behavioral observations as indicators of demographic processes. In particular, I use the regression from a previous study of California sea lion (*Zalophus californianus*) aggression and territorial behavior and reproductive rate to project female abundance at a breeding colony in the Gulf of California, Mexico, over 28 years. I compare these projections to those derived from traditional methods of reproductive rate estimation to analyze the error introduced through the behavioral approximation, and the costs resulting from each monitoring technique.

Description of the Study System

The study system from Chapter III is the California sea lion breeding colony that occurs on the island of Los Islotes in the southern Gulf of California, Mexico. This colony is the most studied population in the Gulf and has been increasing in population since 1980, although the greater Gulf of California sea lion population decreased by 20% from 1993 to 2004 (Szteren *et al.* 2006). California sea lions are a sexually dimorphic, polygynous species that is known to exhibit high levels of philopatry (Berta and Sumich 1999; Hernández-Camacho 2001). Each year, from May to August, female sea lions congregate at this breeding colony to give birth to and nurse their pups (Garcia-Aguilar and Aurioles-Gamboa 2003). By July, most females have given birth and enter estrous

while still nursing their yearling pup (Peterson and Bartholomew 1967; Garcia-Aguilar and Aurioles-Gamboa 2003). The onset of estrous in the females triggers dominant males to form territories on these beaches to defend the resident females from competing males. Although most copulation occurs in the surf, it is suspected that these territorial males compete to mate with the fertile females (Boness 1991). After the breeding season, the female will continue to nurse and care for her yearling pup until the following breeding season begins (Boness and Bowen 1996; Melin *et al.* 2000). By this time the yearling pups have grown to be juveniles and stay in this age class until five years of age (Aurioles-Gamboa and Zavala 1999). As adults, male California sea lions are larger than their female counterparts and have a lower rate of survival (Aurioles-Gamboa 1988; Hernández-Camacho 2001). Mature females have a high survival rate (yearly survival rate of ~0.95; Hernández-Camacho 2001; Hernández-Camacho *et al.* 2008) and typically bear one pup per year (Riedman 1990; Hernández-Camacho 2001). This combination of life history traits is easily modeled by the equations in Chapter III (Gerber 2006; González-Suárez and Gerber 2008).

II. MONITORING BEHAVIOR: ASSESSING POPULATION STATUS THROUGH RAPID BEHAVIORAL ASSESSMENT

Abstract

Despite years of effort from behavioral ecologists, theories of animal behavior have not been integrated into the field of conservation biology. I propose a novel framework to join these fields through the use of demographic models. I present three strategies for incorporating behavior in demographic models, outline the costs of each strategy through decision analysis, and build on previous work in behavioral ecology and demography. I then provide practical recommendations for applying this framework to management programs. First, relevant behavioral mechanisms should be included in demographic models used for conservation decision-making. Second, rapid behavioral assessment is a useful tool to approximate demographic parameters through regression of demographic phenomena on observations of related behaviors. Behaviorally estimated parameters may be included in population viability analysis for use in management. Finally, behavioral indices can be used as warning signs of population decline. Rapid behavioral assessment holds promise as a cost-effective tool, but also represents a cost to model accuracy. I provide a framework for implementing rapid behavioral assessment through case studies of reproductive, foraging, and anti-predator behaviors. My framework combines each strategy through decision analysis to provide quantitative rules that can inform management programs of when aspects of conservation behavior may be beneficial.

Introduction

Despite more than a decade of literature on conservation behavior (Clemmons *et al.* 1997; Caro 1998; 1999; Gosling and Sutherland 2000; Festa-Bianchet and Apollonio 2003; Blumstein and Fernández-Juricic 2010) and a few outstanding case studies (Moore *et al.* 2008), Caro (2007) recently conceded that behavior can only inform specific management programs and no overarching theories may be found to connect the two fields (but see Berger-Tal *et al.* 2011). Here I challenge this claim by providing a framework that applies behavioral knowledge to quantitative conservation biology, namely through population demography. This framework accommodates existing studies in the area of conservation behavior and indicates areas of future exploration.

The relationship between a population's demography and the behavior of its members is the basis of my conceptual framework (Fig. 1). The interactions between behavior and population dynamics can provide structure to conservation programs through demographic models used in population viability analysis (PVA) in three ways: 1) including behavioral mechanisms that increase biological realism; 2) approximating demographic parameters through rapid assessment of behavioral indices; and 3) monitoring for behavioral warning signs of population decline. Decision analysis incorporates insights resulting from these strategies, providing a quantitative method to assess the tradeoff between predictive ability and program cost. This combination of PVA, rapid assessment and decision analysis leads to logical guidelines in applications of behavior to management decisions.

Below I describe three strategies for applying knowledge of animal behavior to demography through PVA. Management implications from these three strategies are interpreted in a cost-benefit analysis to suggest when each strategy might be appropriate. I then detail the process of rapid assessment of behavioral indices as a means to estimate demographic parameters followed by examples of possible applications to three areas of conservation behavior concern: foraging, reproduction and predator avoidance.

A framework for integrating animal behavior into conservation decision-making

Models of population dynamics have been used extensively to make informed conservation decisions in the past (Mace and Lande 1991; Beissinger and Westphal 1998; Beissinger and McCullough 2002; Morris *et al.* 2002) and have become a critical aspect of successful conservation policy (e.g., potential biological removal in MMPA, the Revised Management Procedure under the IWC, and listing under the IUCN Red List and ESA). Demographic models are also suitable tools for describing the feedbacks that may occur between demography and behavior (Fig. 1). First, behavior of individuals can influence demography. For example, dunnocks (*Prunella modularis*) form male-dominated linear dominance hierarchies at winter food patches (Davies 1992). These hierarchies can result in increased rates of female mortality, causing male-biased sex ratios following severe winters (Davies 1992). Demography may also influence the behavior of individuals, as can be seen in the harem-building saiga

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antelope (*Saiga tatarica*). When these animals were more abundant and sex ratios more balanced, males competed for access to harems of females. As a result of intense hunting of male antelope for their horns, some remaining populations have been shifted to extremely female-biased sex ratios. This rarity of male saiga has caused a switch in mating behavior: now dominant females restrict access to rare males (Milner-Gulland *et al.* 2003). This change in behavior may then reduce the fecundity of the population as subordinate females are not able to mate and bear offspring, bringing the relationship between behavior and demography full circle. Managers and conservation biologists can make use of the links between behavior and demography by including them in their predictive models or by using behaviors as indicators of demographic parameters and population trends (Fig. 1).
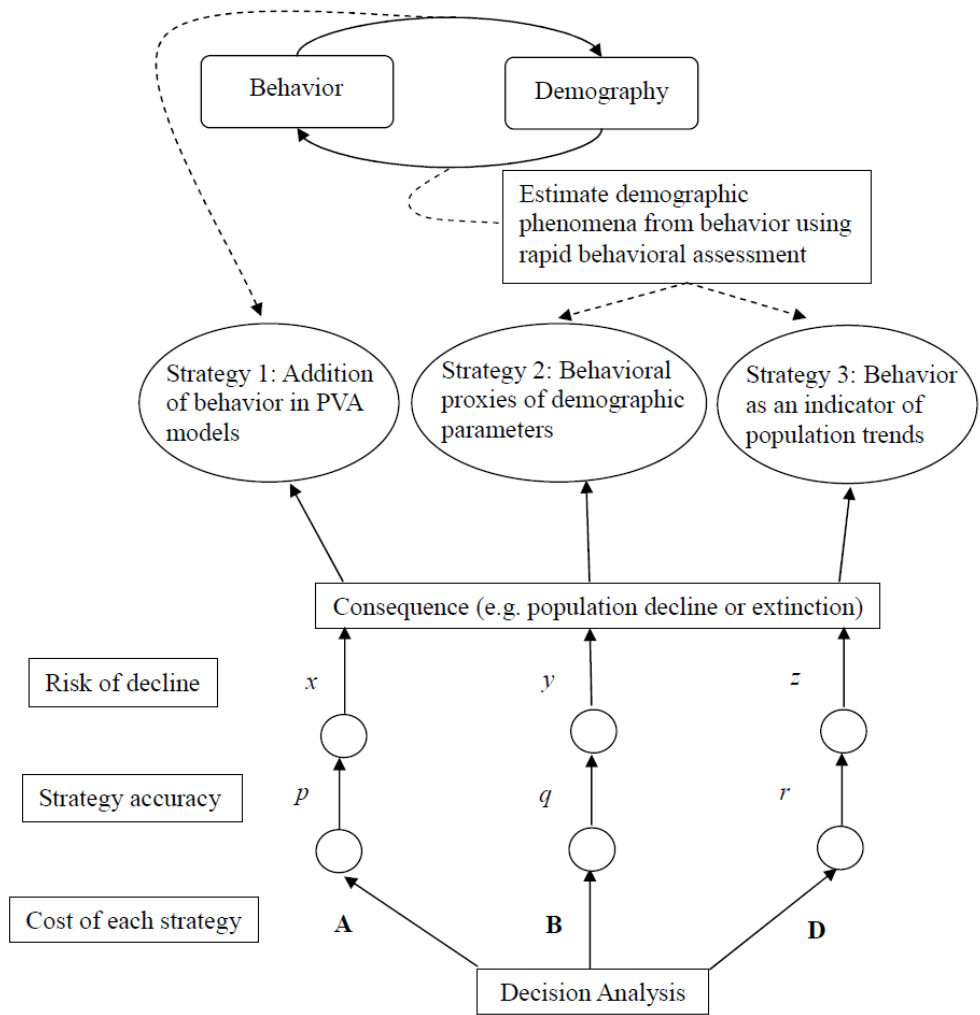
Figure 1: Schematic of the connection between behavior and demography, and three strategies to apply animal behavior to conservation programs. The decision analysis shows how the costs of each strategy ($A > B > D$) combine with the accuracy of each strategy ($p > q > r$) and the predicted risk of population reduction ($x, y,$ and z). Implications from this framework are found in Table 1.

Table 1: Implications of Strategies 1, 2 and 3 on population viability models and program costs. Decision rules resulting from Figure 1 are provided for each strategy and are compared to the costs of traditional monitoring (**T**) and population decline (**C**).

Implication	Strategy 1: Addition of behavior in PVA models	Strategy 2: Behavioral proxies of demographic parameters	Strategy 3: Behavior as an indicator of population trends
Complexity of resulting model	Increased	No change	Decreased
Expected accuracy	Increased	Decreased	Decreased
Cost	Increased	Decreased	Decreased
Choose strategy if:	$px(\mathbf{A}+\mathbf{C}) < \mathbf{T}+\mathbf{C}$	$qy(\mathbf{B}+\mathbf{C}) < \mathbf{T}+\mathbf{C}$	$rz(\mathbf{D}+\mathbf{C}) < \mathbf{T}+\mathbf{C}$

Strategy 1: Including behavior in PVA models

Much attention has been given to describing the inclusion of behavioral phenomena in population models (Sutherland 1996; Hastings 1997; Ebert 1999; Caswell 2001; Morris and Doak 2002). This strategy is already displayed in spatially explicit population models that incorporate dispersal behavior (e.g., González-Suárez and Gerber 2008; Revilla and Wiegand 2008). In addition, when mating behavior is included in population models, it can result in more accurate estimates of population growth rates (Gerber 2006), which may then better inform management decisions and harvest protocols (Horev *et al.* 2012). Greene *et al*. (1998) show that incorporating mating system and paternal care in population models can elucidate the risks of directed harvests in African game animals. The drawback to these additions, however, is that they result in more complicated models, which in turn often leads to increased cost due to the need for parameter estimation (e.g., increased radio tagging of individuals to describe movement behavior or DNA testing for paternity analysis).

This tradeoff between model accuracy and program cost may be best explored with decision analysis (Fig. 1; Table 1). I can compare the costs of observing a behavioral indicator to the cost of the current or traditional method of population management (**T**) and the cost of possible population decline (**C**). If including behaviors explicitly in models results in more accurate descriptions of population dynamics in a threatened system, the benefit to wildlife managers and policy makers may be greater than the extra costs and effort required to create these new models. Therefore, I can compare the probability of increased accuracy

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(p) and the probability of population decline (x) along with the program costs of

Strategy 1 (**A**) to those of the traditional method: choose Strategy 1 if $px(\mathbf{A} + \mathbf{C}) <$

$\mathbf{T} + \mathbf{C}$. In other words, if the increased accuracy and cost of parameter estimation

results in a more accurate estimate of population decline and its consequences,

Strategy 1 should be considered.

Strategy 2: Behavioral observation as a proxy for demographic parameters

It may be possible for conservation biologists to estimate latent

demographic rates through observation of certain behaviors (Fig. 1). The simplest

models of population dynamics describe how birth (b) and death rates (d) interact

to result in populations that change over time. By observing particular behaviors

that are known to be correlated with demographic rates, researchers can uncover

the parameters underlying the dynamics of monitored populations. Wildlife

managers should be able to observe behaviors related to birth (e.g., nursing or

parental care) and survival (e.g., foraging efficiency or predator wariness) and use

them as proxies of the true rates (b and d, respectively). These behavior-based

parameter estimates may then be implemented in PVA models to help make

management decisions at a faster pace than standard surveying techniques.

Instead of increasing costs through model complexity, Strategy 2 may

simply reduce the current cost of monitoring the population of concern. However,

these strategies introduce greater errors in population trajectories due to variance

in the correlation between the behavioral indicator and the true parameter. As

long as this observation error is small in relation to the benefits incurred from

reduced costs in making these parameter estimations (**B**), Strategy 2 may be an

important monitoring option. Here, the accuracy (q) and probability of decline (y)

for Strategy 2 must also result in the inequality: $qy(\mathbf{B} + \mathbf{C}) < \mathbf{T} + \mathbf{C}$ (Table 1);

however, in this case the accuracy and cost (q and $\mathbf{B}$, respectively) are likely to be

smaller than those of Strategy 1 (p and $\mathbf{A}$).

Strategy 3: Behavior as an indicator of population trends

In systems where the behavioral indices from Strategy 2 have consistently

shown associations with population growth, behavioral observations could be

used as rules of thumb to describe qualitative patterns of population trends. In this

case, changes in population size or composition may result in a marked switch

from one behavior to another. Observing these behavioral changes would allow

managers to anticipate the fate of populations and impose management decisions

based on early behavioral warnings. This process would only be acceptable in

areas where behavioral observation and management are well established and the

interaction between behavior and population dynamics is well understood. In the

case of saiga harvesting outlined above, because viable populations of saiga have

been shown to depend on the proportion of adult males (Milner-Gulland

1994;1997), sustainable harvest of males may be restricted to years when

guarding of males is not observed.

Although this strategy is understandably less accurate than detailed

monitoring, it might act as an inexpensive warning flag for wildlife managers. In

the decision analysis, the costs resulting from a false alarm ($\mathbf{D}$) must be minimal

in comparison to the benefits of the early warning <u>and</u> the option of traditional

management with later detection of population decline, or $rz(\mathbf{D} + \mathbf{C}) < \mathbf{T} + \mathbf{C}$.

Rapid Behavioral Assessment

Before Strategies 2 or 3 can be implemented, a clear relationship must be drawn between a behavior and a related demographic phenomenon. Rapid assessment techniques can provide a means to define this relationship by observing the behavioral indices and estimating demographic parameters. Rapid behavioral assessment (RBA), typified by an intensive initial double-sampling (Eberhardt and Simmons 1987) of both the targeted behavior and demographic data followed by continued monitoring of the behavioral index, may provide the data needed to implement Strategies 2 and 3 above (Fig. 2). A study of the chough (*Pyrrhocorax pyrrhocorax*) by Kerbiriou *et al*. (2009) is a helpful example of using RBA for estimating juvenile survival. During their study the researchers observed the spatial distribution and foraging behavior of choughs on Ouessant island in France and monitored monthly survival of juveniles color-banded as fledglings. They found that foraging frequency and juvenile survival were both negatively correlated with tourist visitation (Kerbiriou *et al*. 2009). Kerbiriou *et al*. (2009) argue that this reduction in survival is due to the observed decrease in foraging resulting from human disturbance after fledging. Because data on both foraging behavior and juvenile survival were collected for this population, a clear association could be derived from regression models to describe juvenile chough survival as a function of their foraging habits.

Kerbiriou *et al*. (2009) applied their findings to an individual-based population model and found that the prospective increase in tourism on the island increased the short-term extinction probability of this population due to the

adverse effects of disturbance on foraging and the resulting decrease in juvenile

survival. Similar population models can be constructed using the regression

between this behavior and the demographic parameter to estimate risk to the

population (y or z in Fig. 1). Models using both the behavioral estimate of the

demographic parameter and the traditional parameter estimate can be compared to

quantify the deviation of the RBA model from the traditional demographic model.

Multiple methods of model comparison including information criterion

techniques, comparison of resulting growth rates and probabilities of extinction,

and absolute differences in estimated population sizes resulting from each model

should be used to determine the accuracy of the model that employs RBA. These

tests will also identify any bias resulting from these indirect measures (q and r in

Fig. 1). To the extent that error in the behavioral estimate results from small

sample sizes, the lowered costs from RBA may allow for larger samples, resulting

in lower measurement error, or higher q and r.

I do not expect that this method of parameter estimation will be

appropriate for all demographic parameters as some parameters are more sensitive

to errors in estimation than others. Therefore, I suggest that RBA may be most

useful for estimating parameters with low to moderate model sensitivities. This is

because error introduced through regression will become magnified in highly

sensitive parameters, but for parameters with little sensitivity there is no need for

such detailed estimates.

Even if estimates resulting from behavioral observations are sufficient in

predicting population trajectories, costs of including RBA or other behavioral

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information in PVAs must be low enough to justify their inclusion in future

censuses and management plans. As an example, the estimated cost of a 2007

field study by L. Gerber to estimate reproductive rates in California sea lions

(*Zalophus californianus*) in the Gulf of California, Mexico, was approximately

US$4,992 (equal to **T** in the decision analysis). This amount included local

transportation, tagging materials, and camping gear for five people for three field

trips, each lasting nine days, during the summer of 2007. This figure also includes

the cost of a second trip to collect resighting data later that winter. The

approximate cost of a single trip to collect only data on aggression behavior for

the same year would be **B** = $2,790. Although the first amount would be required

for the initial double sampling of behaviors and demographic data, monitoring

efforts in following years may be similar to those of the latter value. Provided that

behavioral observations can be made relatively easily and through cost-effective

means, the tradeoff between accuracy and cost per unit effort may justify the use

of RBA.

Because many studies have described systems where Strategy 1 is

important for conservation, I focus the remainder of my review on examples of

Strategies 2 and 3. Specifically, I characterize three areas of vertebrate animal

behavior that greatly influence the viability of populations: reproduction,

foraging, and anti-predator behaviors. Within each section I provide case studies

of systems amenable to Strategy 2 or 3 and where RBA may prove to be a useful

monitoring technique. I acknowledge that these examples stem from studies of

birds and mammals, but are confident that the basic relationships between

behavior and demography permeate through a broad scope of animal taxa,

including arthropods, reptiles, amphibians, and even mollusks (Payne *et al.* 2011).

Step 1: Find an efficient and cost-effective way to measure a possible behavioral indicator of population status.

⇩

Step 2: Assess the accuracy of RBA through double-sampling analysis and regression of both the behavioral indicator and demographic parameter (quantify q in Fig. 1).

⇩

Step 3: Compare predictions of population trajectories from behavioral PVA models to those from PVA models using traditional parameter estimation (compare y to traditional risks of population decline).

⇩

Step 4: If the tradeoff between the cost and accuracy of rapid behavioral assessment is acceptable, continue to monitor this behavior for changes in population viability (assess $qy(\mathbf{B}+\mathbf{C}) < \mathbf{T}+\mathbf{C}$ from Fig. 1).

Figure 2: Steps for implementing rapid behavioral assessment into the monitoring and management of an animal population.

Reproductive Behavior

The behaviors surrounding reproduction, parturition, and parental care are closely related to rates of reproduction and offspring survival. In particular, behaviors stemming from the mating system may have implications for female fecundity and ultimately population growth rates (Gerber 2006). It has also been proposed that small populations, which typically have high conservation priority, may be limited by male fecundity as well as that of females (Gerber 2006; Rankin and Kokko 2007). These male fecundities will most likely be easier to estimate through correlation with mating behaviors rather than explicit testing of male paternity, though the costs surrounding estimation of these rates may be prohibitive for many conservation projects. I therefore focus on female fecundity in the following examples.

Strategy 2 – Gerber *et al*. (2010) have shown that female reproductive rates are correlated to rates of male and female aggression in California sea lions observed in the same year of fecundity estimation. Rapid assessment of male aggression and other territorial behaviors, harem and territory sizes, or patrolling activity, may provide a fast and cost-effective means to estimate female, and possibly male, fecundities. Combining these behaviorally-assessed parameters with PVA models may provide managers and policy makers with relatively accurate island-specific estimates of California sea lion population growth at a considerably lower cost. Initial investigations that include parameters from RBA suggest that behavioral proxies of reproductive rates in these sea lion populations provide an adequate means to predict risk of population decline (Chapter III).

Monitoring these and other behaviors through RBA may allow managers to focus conservation programs on at-risk subpopulations rather than spreading efforts across the entire population.

Strategy 2 – In a long-term study of bearded vultures (*Gypaetus barbatus*) in the Spanish Pyrenees, Carrete *et al*. (2006b) correlated the occurrence of polyandrous breeding nests with habitat saturation. They found that as the population of bearded vultures grew and traditional monogamous breeding pairs claimed available territories, breeding trios composed of one dominant male, one subordinate male and a female began to be established in older, more productive breeding territories. This change from monogamous to polyandrous nests was also highly correlated with a reduction of fecundity per nest in these traditionally productive breeding pairs, which reduced the productivity of the population as a whole (Carrete *et al.* 2006b). In this system, where frequency of polyandrous nests and nest productivity is known, RBA of nest mating systems may prove useful in estimating fecundity of the population. It may be possible to assess population viability from these estimates for future management action.

Strategy 3 – To further the example of the bearded vulture (Carrete *et al.* 2006b), the onset of polyandry may be an indicator of a demographically robust population where all available habitat has been filled through increasing vulture abundance. In contrast, if this habitat saturation is facilitated by supplementary feeding by wildlife managers, which may reduce dispersal of young vultures, a switch to polyandry near these supplementary feeding points may serve as a signal to stop supplementary feeding to encourage dispersal (Carrete *et al.* 2006a).

In systems such as this and the saiga antelope from the example above, well defined shifts in mating strategy can serve as signals of population status for wildlife managers and conservation policy makers.

Foraging Behavior

Optimal foraging theory indicates that in a predictable environment there is generally one optimal foraging pattern (Pyke *et al.* 1977), which is manifest in the role and distribution of individuals within a population. As the environment becomes less predictable due to a number of pressures, foraging patterns tend to change. These environmental pressures can be biotic in origin and include small population densities of threatened species (Reed 1999), a reduction in important cues that may indicate high patch quality (Reed 1999), increased predation risk (Heithaus *et al.* 2007), or poaching (Donadio and Buskirk 2006) to name a few. Abiotic pressures (e.g., temperature, nutrient content, or amount of cover) may also result in changing foraging patterns. Often these environmental pressures combine in tradeoffs between foraging and other vital processes, such as reproduction or evading predation. Because these optimal foraging behaviors are predictable given information about the animal's environment, the vital rates they are correlated with should be predictable also. Sutherland (1996) provides detailed explanations and applications of foraging theories to population models.

Strategy 2 – The pressures, or costs, surrounding foraging are three-fold: energetic costs (E), the cost of predation (P), and the cost of missed opportunity (M), and are directly related to harvest rate (H) by the equation: $H = E + P + M$

(Morris *et al.* 2009). The density of food in a patch at which harvest rate satisfies this equality is the giving-up density (GUD; Brown 1988). From this equation we see that as risk of predation while foraging in the patch increases, so does the GUD (Olsson and Molokwu 2007). Alternatively, in food-scarce habitats, the GUD of a patch will likely be lower (Olsson and Molokwu 2007) because of the heightened energetic requirements of the foraging individuals. By presenting animals in a population with experimental patches, the foraging animals provide information about the level of environmental pressure in their habitat.

Olsson *et al*. (1999) applied this sampling technique in a population of threatened lesser spotted woodpecker (*Dendrocopos minor*) and found that average GUDs were correlated with individual reproductive success. They showed that individual woodpeckers that left foraging patches with lower densities of wood-inhabiting insect larvae also initiated egg laying later than those that left patches at higher prey densities (Olsson *et al*. 1999). High levels of GUD were also significantly associated with higher rates of offspring fledging that year. The researchers conclude that high individual GUDs may be an indicator of individual reproductive success. Importantly, these GUDs were observed weeks to months before the onset of breeding in the spring. By monitoring GUDs in this population late in the winter, managers may be able to predict reproductive output of the population later that year, allowing time for mitigation should GUDs decrease under an acceptable threshold.

Strategy 3 – Many studies have been conducted to describe the optimal feeding patterns involved in domestic animal husbandry. These optimal patterns

have been linked to reproductive success and fawn survival in domestic sheep (McEvoy and Robinson 2002). McEvoy and Robinson (2002) describe that variation between foraging extremes, or a stuff-starve foraging pattern, during pregnancy may lead to lower embryo survival, reducing reproductive output. Nutritional content of forage during gestation is also crucial for offspring survival and may compromise ovary development in unborn females (Yakovleva *et al.* 1997; Nazarova and Evsikov 2008). Similar or more pronounced patterns are likely to appear in avian and reptile taxa, as they must provision offspring with all required nutrients before egg laying (Martínez-Padilla 2006; Nelson *et al.* 2010). In birds, these behaviors may be used to monitor fledging success of breeding pairs. Mariette *et al*. (2011) found that visitation rates at local feeders by zebra finches (*Taeniopygia guttata*) predicted crop contents in nestlings – a possible indication of nestling fledging and reproductive success of the parental pair. By monitoring foraging frequency and choice of forage preceding and during the breeding season of a target species, managers may quickly recognize the possibility of compromised reproduction or offspring survival due to malnutrition before the effects are observed in the following year(s). If these sub-optimal foraging patterns are observed, conservation decisions can be made preemptively to avoid possible reproductive collapse.

Anti-predator Behavior

Anti-predator behaviors, such as flight response and vigilance, often reflect an animal's previous exposure to predation. Therefore, animals

experiencing these dangerous situations should be more wary of their surroundings compared to naive individuals. Observing and quantifying these fear behaviors through rapid assessment may give conservation personnel a more accurate measure of the level of experience a focal population has with predation. Although these behaviors are termed "anti-predator" behavior, in many cases these behaviors are displayed in response to human-induced threats.

Strategy 2 - To estimate the amount of experience animals had with human contact, Caro (2005) recorded the reaction of African mammals to the presence of his vehicle inside and outside of the protected Katavi National Park. He found that many species became more wary or fled from the vehicle more often outside of the park – where hunting pressure is known to be higher – than inside its boundaries. Donadio and Buskirk (2006) apply this hypothesis further, suggesting that flight response may serve as an indicator of poaching pressure. They recorded the distance and frequency that groups of guanacos (*Lama guanicoe*) and vicuñas (*Vicugna vicugna*) fled from researchers standing in the bed of a truck driving past the heard. They found that the animals fled more frequently in areas suspected of higher poaching rates due to less protection from law enforcement (Donadio & Buskirk 2006).

Surveying these flight behaviors through rapid assessment may provide estimates of survival probability in these herds. Also, if estimates of both legal hunting and poaching pressures exist, managers may be able to model the effect of poaching on population persistence. These estimates can then be integrated into PVA models to direct management decisions on anti-poaching policies.

Strategy 3 - Human-induced stresses may not always come in the dramatic form of poaching. In a world of increasing ecotourism, some conservation biologists have started to question the effect of human disturbance in visited populations (Frid and Dill 2002; Blumstein and Fernández-Juricic 2010). Similar to the chough in the example above, European shag (*Phalacrocorax aristotelis*) are costal breeding sea birds that are threatened by disturbance to foraging juveniles (Velando and Munilla 2011). Velando and Munilla (2011) show that foraging European shag at the Cíes islands in Galicia, Spain are highly disturbed by the presence of boats in important foraging patches. They find that the birds group closer together and reduce foraging dives drastically as the number of boats increases (Velando & Munilla 2011). By monitoring foraging patches for dense groupings of European shag, action may be taken to reduce disturbance levels and therefore mitigate future loss of juvenile birds. Observation of disturbance behaviors such as this and their effects on population growth may prove important in guiding management programs and policy in these tourism destinations.

Discussion and Conclusions

I provide a conceptual framework that is rooted in previous studies of animal behavior and population dynamics to provide structure for applying behavioral studies to conservation decision-making. I have outlined three strategies to aid conservation biologists in integrating this knowledge into their management programs with emphasis on the areas of reproductive, foraging, and anti-predator behaviors. In particular, Strategy 1 incorporates behaviors explicitly

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into demographic models. Strategy 2 assumes that behaviors and demographic parameters are correlated and makes use of this relationship to estimate the latter from the former through rapid behavioral assessment. Strategy 3 uses these behavioral indicators as warning flags against population decline. Because these three strategies, their associated models, and the actions they require can be combined into decision analysis, the above framework not only makes use of behavioral ecology theory, but also provides general rules for when incorporating behavior into management is beneficial.

My framework and particularly the technique of RBA are methods that should lead to reduced costs over the course of a monitoring program. The examples of RBA provided above are only a small sample of the wealth of knowledge behavioral ecology theory has brought to the attention of behaviorists and conservationists alike. A more detailed list of behaviors and their conservation implications can be found in Table 2, though I do not intend for this list to be an exhaustive representation of these important relationships. My approach is not intended to replace standard methods of population parameter estimation, as these provide the most accurate accounts of species abundances and are the basis of the models used in PVA. I recognize that such methods are essential for wildlife management and provide invaluable data on population status and viability. I envision an adaptive management approach that incorporates RBA into monitoring procedures in conjunction with traditional demographic parameter estimation. In this context, RBA may prove to be an acceptable tool for making fast and efficient management decisions.

Though population demography is only one aspect of conservation biology, I believe that its wide-ranging application in policy and management provides an appropriate means of including demographic ties to behavior. My conceptual framework allows future management programs to make the most of behavioral and population dynamic information with the benefit of decreased program costs. I hope this work helps conservation behavior in saving both species and money.

Table 2: Implications of animal behavior for population demography and population viability analysis, including behavioral data that can be collected to estimate PVA parameters.

Behavior		Implication for PVA	Data collection	References
Reproduction	Mating system	Fecundity Sex ratio Patch choice Genetic diversity	Type, # of mates, mating rates, location, time, frequency	Shuster and Wade 2003; Carrete *et al.* 2006b; Gascoigne *et al.* 2009; Jenouvrier *et al.* 2010
	Mate choice, mate competition, mate guarding	Genetic diversity Fecundity Cost: energetic and predation pressure	Paternity, cryptic choice, which mates are selected, # of fights/displays, # of successful matings, time spent guarding, # of mates	Cooper and Vitt 2002; Matsubara 2003; Clutton-Brock 2007;2009
	Dispersal	Immigration/ emigration Genetic diversity, inbreeding Cost: risk of dispersal	Rate, survival, which populations to/from	Peacock and Smith 1997; Sterck *et al.* 2005; Randall *et al.* 2007; Robbins *et al.* 2009
	Parenting	Fecundity, mating success	Duration, effort, success	Trivers and Willard 1973; Jennions and Polakow 2001
Foraging	Diet choice	Survival: Prey availability Cost: New predation pressures, infection risk	Forage type, nutrient quality	Coolen *et al.* 2007; Heithaus *et al.* 2008
	Patch choice	Immigration/ emigration	Type of patches, rate of movement, length of stay	Sutherland 1996; Heithaus *et al.* 2007; Kerbiriou *et al.* 2009

Table 2 cont'd

Behavior		Implication for PVA	Data collection	References
Foraging	Rate/Time	Cost: Predation pressures, nutrient values Carrying capacity	When, how often, and how much	Sutherland 1996; Morris and Mukherjee 2007; Mariette *et al.* 2011; Oppel *et al.* 2011
	Missed opportunity	Survival: Food availability Cost: Predation pressure	Giving-up density	Whelan and Jedlicka 2007; Morris *et al.* 2009
Anti-Predator	Flight	Cost: Poaching, predator avoidance Survival	Distance from predator, time before flight	Caro 2005; Donadio & Buskirk 2006
	Predator inspection, detection and vigilance	Cost: Re/introduced predator species Survival Growth rate Group size	Distance, how inspection happens, who inspects, inspection/detection rate, size of group, who keeps watch, accuracy	Manor and Saltz 2003; Mooring *et al.* 2004
	Generalization and Discrimination	Cost: Re/introduction of predators Survival	Rate of learning, accuracy	Griffin *et al.* 2000; Coleman *et al.* 2008; McCleery 2009
	Disturbance	Cost: missed opportunity Survival	Distance, recovery, types of disturbance	Manor and Saltz 2003; Blumstein *et al.* 2005; Velando and Munilla 2011

III. WHAT DOES ANIMAL BEHAVIOR TELL US ABOUT POPULATION VIABILITY? RAPID BEHAVIORAL ASSESSMENT OF CALIFORNIA SEA LIONS IN THE GULF OF CALIFORNIA, MEXICO

Abstract

There is an acute need in conservation management for cost-effective approaches to estimate population viability. In this chapter, I examine the application of rapid behavioral assessment (RBA), a novel method recently proposed that employs behavioral information as an affordable proxy of costly demographic parameters. Specifically, I use RBA to estimate birthrates for use in population viability analysis (PVA) of a breeding colony of California sea lions (*Zalophus californianus*) in the Gulf of California, Mexico. This approach implies a tradeoff between a less costly method of estimating birthrates and increased model error. To investigate the effects of using the RBA estimate of birthrate, I project female abundances using two matrix model structures and multiple parameter estimation methods and compare model outputs to census data spanning 28 years. I also perform a cost analysis of the proposed and traditional techniques. I find that models using RBA overestimate female abundances when compared to standard methods of birthrate estimation; however, projections from behavioral models are still conservative when compared to theoretical birth function approaches. Thus, rapid behavioral assessment may provide a promising and cost-effective approach to monitoring changes in demographic rates. I conclude with a discussion of general guidelines for the future use of rapid behavioral assessment in conservation management.

Introduction

Conservation managers and policy makers must make decisions about biodiversity conservation in the face of limited funding for data collection. Population viability analysis (PVA) has become a widely used approach to compare the relative risk among populations, to identify critical life stages, and to prioritize management actions (Mace and Lande 1991; Beissinger and Westphal 1998; Beissinger and McCullough 2002; Morris *et al.* 2002). These PVAs require some estimate of the population size and estimates of demographic rates such as birth and death rates, which managers use to project future abundances or estimate probabilities of decline (Caswell 2001; Morris and Doak 2002). These estimates, however, can be costly and time consuming to obtain, and also have the possibility to change over the course of the program (Chirakkal and Gerber 2010). Thus it is of critical importance to identify cost-effective approaches to estimating demographic rates to facilitate effective decision-making in managing wild populations (Peterman and Anderson 1999; Drechsler and Burgman 2004).

I recently proposed rapid behavioral assessment (RBA) as an approach to minimize the cost of population monitoring through PVA (Chapter II). RBA relies on the potential correlation existing between particular behaviors such as foraging or establishing breeding territories and related demographic phenomena (Olsson *et al.* 1999; Kerbiriou *et al.* 2009; Gerber *et al.* 2010); therefore observing related behaviors may allow managers to estimate the survival and reproductive rates of a focal population. The RBA technique utilizes double sampling (Eberhardt and Simmons 1987) of data on a demographic parameter (i.e., survival estimated

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through mark-recapture) and a related behavioral indicator (i.e., predator vigilance) to describe a relationship between the two. With an established relationship between particular behavioral and population parameters, monitoring of the behavioral indicator may be used to inform parameter estimates for PVA models.

Because observations of behavior generally require lower costs or effort than more intensive and invasive demographic studies, this monitoring tool may reduce the cost of wildlife monitoring. However, there is a tradeoff in RBA between decreased program cost and resulting decreased accuracy of the demographic models. This reduced accuracy results from the error variance in the regression of the demographic parameter on the behavioral indicator. Monitoring programs should therefore only use behavioral observations to estimate model parameters when this error is minimal, otherwise decisions made using the RBA estimate may increase the risk of population decline (Chapter II).

Here, I apply the RBA protocol to make predictions of the population dynamics of a California sea lion (*Zalophus californianus*) colony, and I explore the trade-offs between projection accuracy and cost of estimation. For this purpose I develop multiple combinations of model formulation and parameter estimation techniques, including RBA, and compare these projections to census data. The breeding colony occurs on the island of Los Islotes in the Gulf of California (GoC), Mexico, and is one of the best studied subpopulations in the Gulf. In a previous study, Gerber *et al*. (2010) described a relationship between sea lion reproductive rates and observed aggression rates and male territory sizes

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at breeding colonies within this population. From the regression in this study, I estimate female fecundity on Los Islotes from behaviors observed in July from 2004 to 2007. This fecundity estimate was used in population models to project female abundances over a 28-year span from 1980 to 2008, a period that includes 24 census years.

Because my goal is to describe the influence of RBA estimates in PVA, and because there are many aspects of viability analysis, I compare projections through multiple perspectives. First, I construct one- and two-sex matrix models to investigate the importance of including males in the models. As many have argued (Gerber 2006; Rankin and Kokko 2007), two-sex models may result in different population dynamics as compared to traditional models that only follow the female portion of the population. I also include males in my models because two methods of birthrate estimation explicitly involve males in their calculations. These two methods include the technique of RBA where male aggression is negatively correlated with reproduction due to possible trampling of pups (Gerber *et al.* 2010), and theoretical birthrate functions, which estimate fecundity from simple ratios of male and female abundance. In each case, I compare population projections to those that result from models calculated using the traditional method of birthrate estimation. I consider these models based on demographic counts to be the most accurate estimates of birthrate because they involve the most direct method of estimation (Beissinger and Westphal 1998; Coulson *et al.* 2001). Stochasticity is included in each model/estimate combination by choosing from a list of previously estimated parameter values for this population and

resulting distributions from each combination are compared. In order to address the accuracy *vs.* cost trade-off, I perform a cost analysis of each technique and relate these to the accuracy of each models' predictions. From my comparisons I make conclusions about the utility of alternative methods of birthrate estimation when more detailed, count-based estimates are not available or their costs are prohibitive. I also make general conclusions about when RBA is useful and provide guidelines for future applications of this technique.

Methods

Study system

I model the population dynamics of a breeding colony of California sea lions (*Zalophus californiaus*) on the island of Los Islotes in the GoC, Mexico (Szteren *et al.* 2006). This is one of the best studied breeding colonies in the GoC, with the most recent observations spanning from 2004 to 2008. These last censuses indicate an increasing population on this island; however the greater GoC population of California sea lions has seen a 20% reduction in numbers between 1993 and 2004 (Szteren *et al*. 2006). California sea lions in the GoC give birth and breed during the summer months between May and August (Garcia-Aguilar and Aurioles-Gamboa 2003). By July most pregnant females have given birth to a single pup, and males have formed what are thought to be breeding territories among the females (Riedman 1990). Around one month after parturition, females enter estrous and mate (Peterson and Bartholomew 1967; Garcia-Aguilar and Aurioles-Gamboa 2003). The yearling pups will stay with

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their mothers until they reach one year of age and their mothers give birth again

(Melin *et al.* 2000; Garcia-Aguilar and Aurioles-Gamboa 2003). After weaning,

the young are considered to be immature juveniles from years one to four

(Aurioles-Gamboa and Zavala 1999). At five years of age, females become

sexually receptive and males begin competing for mates (Peterson and

Bartholomew 1967). This life history pattern is well represented by a stage-

specific, discrete-time matrix model that estimates population size after

parturition in July.

Developing population models

     I develop a set of six population models that incorporates model structure

variations in three aspects (Table 3): a) sex structure; b) birth rate estimators; and

c) stochasticity. I compare a one-sex, female-based model to a more complex

two-sex model. The one-sex model reflects the female portion of the population in

3 stages: pup (P), juvenile (J), and adult female (F). Survival of pups (S_P) through

their first year results in their graduation into the juvenile class, joining the

surviving immature juveniles (S_J). As juveniles survive and mature, they grow

(G) to become adult females. Adult females survive with the probability S_F into

the next breeding season. Birthrate (B) describes the number of yearling pups per

female averaged across the study population. New pups born each year are

multiplied by an even female sex ratio (SR = 0.5), so that I only follow the female

portion of the population. The equations for the one-sex model are:

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$$P_{t+1} = I * B * F_t * SR$$
$$J_{t+1} = S_P * P_t + S_J * J_t \qquad (1)$$
$$F_{t+1} = G * J_t + S_F * F_t$$

$$I = \frac{1}{(1 + (N_t / K))} \qquad (2)$$

where N_t is the total population and the resulting process matrix is:

$$\begin{bmatrix} 0 & 0 & I*B*SR \\ S_P & S_J & 0 \\ 0 & G & S_F \end{bmatrix} \qquad (3)$$

The I term (Eqn. 2 and 5) reflects a form of logistic density dependence that discounts the overall pup birthrate as the total population size reaches and exceeds the carrying capacity parameter K (Dobson and Lyles 1989). I include density dependence in pup births because as the population grows, space on haul-out beaches becomes scarce and animals must climb over others to reach the waterline. This jostling can result in the trampling of young pups, resulting in lower effective birthrates with increasing population sizes (González-Suárez and Gerber 2008).

Because the carrying capacity parameter ultimately acts as a scalar of the combination of other parameters in the model, final maximum population size is highly dependent on the value chosen for K. For this reason I first found the best estimate of K for the model using a demographic estimate of birthrate because this model should reflect true population dynamics best (Beissinger and Westphal 1998; Morris and Doak 2002). Each best K estimate was found by calculating the sum-of-square value (Hilborn and Mangel 1997) of each model to the census data

from 1980 to 2008. I searched over a range of possible K values between 1 and 600 and summed across simulations within each candidate value of K. The value of K resulting in the smallest sum-of-square value is considered to be the best estimate for that model.

I also construct a two-sex model to reflect the entire population over the simulated period. Males are included in this model because it has been argued that the male portion of the population may significantly influence population dynamics (Caswell 2001). Gerber (2006) found that two-sex models reflect actual growth rates more closely than their one-sex counterparts in this sea lion population. This formulation is also necessary for use of a theoretical birth function to estimate birthrates (see *Estimating birthrates*).

The two-sex model divides juveniles entering the adult stage according to the female sex ratio into the adult female (F) and adult male (M) stages. Therefore, the pup and juvenile stages are comprised of both male and female individuals. This is a reasonable assumption because past studies have not found significant differences in survival based on sex in sea lion pups or juveniles at this island (Hernández-Camacho *et al*. 2008). The resulting two-sex model is:

$$
\begin{aligned}
P_{t+1} &= I * B * F_t \\
J_{t+1} &= S_P * P_t + S_J * J_t \\
F_{t+1} &= G * J_t * SR + S_F * F_t \\
M_{t+1} &= G * J_t * (1 - SR) + S_M * M_t
\end{aligned}
\tag{4}
$$

$$
I = \frac{1}{(1 + (N_t / K))}
\tag{5}
$$

where N_t is the total population. The resulting process matrix is:

$$
\begin{bmatrix}
0 & 0 & I*B & 0 \\
S_P & S_J & 0 & 0 \\
0 & G*SR & S_F & 0 \\
0 & G(1-SR) & 0 & S_M
\end{bmatrix}
\qquad (6)
$$

Carrying capacity for the two-sex model (K = 508) was estimated

similarly to the one-sex model (K = 294). These estimates are reasonable because

the ratio of females to the total population (294/508 = 0.579) is similar to that

found in the census data (mean ratio = 0.632). These K values are then used in the

other corresponding models for data analysis. Because of the addition of males to

the model and the change in carrying capacity, the one- and two-sex models

cannot be compared directly in terms of total animal abundance.

Table 3: Models 1 – 6 were composed of combinations of one- and two-sex

matrix models with either the standard demographic birthrate estimate, the RBA

estimate, or a theoretical estimate. Stochastic forms of these models were created

by drawing from previously published parameter estimates or observed data.

Model #	Sexes in model (1 or 2)	Birthrate estimate
1	1	Demographic
2	1	Behavioral
3	2	Demographic
4	2	Behavioral
5	2	Harmonic Mean
6	2	Modified Harmonic Mean

Estimating birthrate

I implement birthrates estimated from demographic and behavioral data and theoretical birth functions in each model described above. The most recent demographic birthrate estimate is calculated as the ratio of pups to females observed at Los Islotes in July between 2004 and 2007. This demographic estimate is used in tandem with previously estimated fecundity values (Table 4) in both the one- and two-sex models (Models 1 and 3, respectively; Table 3); each of which act as the "null" model for comparison with other methods of birthrate estimation.

I also estimate birthrate through RBA using observations of aggression and territory size as behavioral indicators. These behaviors are suspected to be related to birthrate because male aggression generally results from intrasexual competition for breeding territories (Jacobs *et al.* 2008), whereas female aggression is thought to result from mothers protecting their offspring from overcrowding (Heath 1989; Gerber *et al.* 2010). Gerber et al. (2010) observed aggression displays of males and females at six breeding colonies in July of 2004 – 2006 using scan samples. They also measured territory size of individual males at these colonies. Pup and adult female counts were performed at the same time as the behavioral observations at each island. From these data, they described the relationship between these behaviors and demographic calculations of birthrate with the following regression:

$$B = 1.277 + 0.074 * A_F - 0.170 * A_M - 0.001 * Terr \qquad (7)$$

Here, birthrate (B) increases with increasing female aggression (A_F), likely due to

females protecting their young pups from others. In contrast, birthrate is

negatively correlated with male aggression (A_M) and male territory size (Terr),

which is likely due to increased risk to pups from highly territorial males. This

equation is used in both one- and two-sex models (Models 2 and 4, Table 3) to

test if RBA results in similar predictions as the demographic models.

In addition to demographic and behavioral estimates, I also estimate

birthrate through two theoretical birth function models. The first theoretical model

(Model 5) uses the harmonic mean birth function defined by Caswell (2001):

$$B = \frac{2 * M_t}{M_t + (F_t/h)} \qquad (8)$$

Here, birthrate is a function of the number of adult males and females. I use the

polygynous form of this function, which divides females into harems (h) defended

by males. I also analyze a second birth function (Model 6) that was proposed

more recently by Legendre (2004) as a modification of the harmonic mean birth

function:

$$B = \min\left(1, \frac{2 * M_t}{M_t + (F_t/h)}\right)_, \qquad (9)$$

which limits the birthrate at a maximum of one pup per female. This modified

harmonic mean birth function reflects the life history of California sea lions more

accurately than Caswell's harmonic mean birth function because female sea lions

rarely produce twins (Riedman 1990). These two birth functions are only used in

the two-sex models because they require both male and female abundances to calculate birthrate.

These different model formulations result in six models: two demographic (one- and two-sexes), two behavioral (one- and two-sexes), and two two-sex birth function models (one harmonic and one modified harmonic). Table 3 summarizes the forms of these models.

Model stochasitcity

Stochasticity is incorporated into each of the six models in Table 3 by randomly selecting either from parameter estimates published in previous studies or from observed behaviors or harem sizes. Four different estimates of pup, juvenile, and adult survival and birthrate were gained from the literature. Only two estimates of juvenile growth rates were available from previous studies. All rates had been estimated within the census period either in the Los Islotes population itself or from the larger GoC population. Models using alternative estimates of birthrate select from behaviors or harem sizes observed by Gerber between 2004 and 2007 (unpublished data). I limit the number of these alternative birthrate estimates to four to control for the possible benefit of increased model information. Because the RBA estimate of birthrate incorporates three different yet possibly correlated behaviors, I restrict the model to select all three behaviors from the same year (i.e. male and female aggression and territory size from 2005 are always used in Eq. 7 at the same time).

These demographic parameters are randomly selected with replacement in each year of the model and placed into the process matrix to project the population into the next year. Each model is initiated with the abundances of each stage observed in 1980 and simulated 20,000 times. It should be noted that the nature of the stochastcity introduced in each model varies due to the variety of parameter estimates used. Therefore the stochasticity included in the models may be composed of any combination of sampling, spatial, intra-annual and inter-annual variability. In the case of birthrates estimated from behavioral metrics, the employed regression comprises three years on six different colonies and thus includes all of these sources of variability.

Data analysis

I compare the projections of each model to data collected at Los Islotes between 1980 and 2008, which includes a total of 24 census years. Models are initialized with the abundances of each stage observed in 1980. Because of the population size differences in each model due to the addition of males in two-sex models, all comparisons are made using female abundances instead of total population sizes.

I expect that RBA will be most effective when used on vital rates with low to moderate elasticity because parameters with high elasticity will be very sensitive to error introduced through the variance of the RBA regression (Morris and Doak 2002). I therefore calculate the elasticities of the final abundance of adult females after 28 years for each model to a 5% increase in each parameter.

Here, each possible parameter estimate for a single demographic rate was increased by 5% and chosen at random for a total of 20,000 iterations per demographic rate. Elasticity was calculated as $E = (\Delta F_{2008}/F_{2008,\text{original}})/0.05$.

The accuracy of each model is evaluated in two ways. I compare mean log-growth rates resulting from diffusion approximation (Dennis *et al.* 1991) of each model to each other and that computed from a diffusion approximation performed on the census data. I also directly calculate the sum-of-squared deviations (SS score, Hilborn and Mangel 1997) of log-transformed projected female abundances compared to observed abundances in each census year. For each model, the SS score and the percent predicted abundance compared to the observed abundance in 2008 are each calculated for all model simulations. Because these distributions of these indicators violate the assumption of equal variance, all comparisons are made through one-way ANOVA. Indicators with significantly different means were investigated with Games-Howell post hoc tests.

To investigate the effect that uncertainty in carrying capacity has on model predictions, I also plot the goodness-of-fit profiles of each model from the data evaluated over a range of K values between 1 and 600. I then center each plot at the best K estimate for each model (Fig. 4). The model with the least amount of change in sum-of-squared deviations as K deviates from the best estimate is considered more robust to uncertainty in this parameter.

Finally, I present a cost analysis of the traditional and RBA methods of birthrate estimation in relation to their predictive ability. For each behavior or census observation, I calculate effort as the time spent per observation per day.

This calculation was performed for the most recent demographic birthrate estimates from Gerber *et al.* (2010). For the RBA technique, I calculate these values separately for aggression observations and territory size measurements and then take their sum. Plotting these estimation efforts against the resulting model accuracy allows me to compare each model's relative cost.

Table 4: Variables and parameters used in each of the six models with

descriptions and estimates.

Parameters and variables	Description	Values or equations
P_t	Number of pups (individuals from 0-1 year old) at time t	Eq. 1 or Eq. 4
J_t	Number of juveniles (individuals from 1-4 years old) at time t	Eq. 1 or Eq. 4
F_t	Number of adult females (individuals greater than 4 years old) at time t	Eq. 1 or Eq. 4
M_t	Number of adult males (individuals greater than 4 years old) at time t	Eq. 4
N_t	Total population size at time t	$N_t = P_t + J_t + F_t$ (+ M_t, for the two-sex model)
SR	Female sex ratio at birth	SR = 0.5
S_P	Survival rate of pups	$S_P = [0.752^a, 0.437^b, 0.706^c, 0.76^d]$
S_J	Survival rate of juveniles	$S_J = [0.902^a, 0.147^b, 0.656^c, 0.915^d]$
S_F	Survival rate of adult females	$S_F = [0.909^a, 0.95^b, 0.976^c, 0.90^d]$
S_M	Survival rate of males	$S_M = [0.746^a, 0.95^b, 0.881^c, 0.70^d]$
G	Growth rate of juveniles to adults	$G = [0.478^b, 0.219^c]$
I	Discount factor that represents the density-dependent risk of trampling for pups	Eq. 2
K	MLE estimate of carrying capacity at Los Islotes for the demographic estimate of birthrate	One-sex model: 294 Two-sex model: 508
B	Birthrate: number of pups born from an adult female per year	Demographic: $B = [0.825^e, 0.635^a, 0.456^b, 0.63^d]$ RBA: Eq. 7 Harmonic mean: Eq. 8 Modified harmonic mean: Eq. 9
A_F	Average rate of female aggression per hr	$A_F = [1.019, 2.633, 3.469, 3.776]$
A_M	Average rate of male aggression per hr	$A_M = [2.041, 4.571, 1.776, 4.878]$

Table 4 cont'd

Terr	Average male territory area (m^2)	Terr = [158.771, 102.691, 95.949, 93.818]
h	Average harem size observed on Los Islotes	h = [5.453, 3.836, 4.698, 5.595]

[a] *Hernández-Camacho et al. 2008*

[b] *Weilgus et al. 2008*

[c] *Hernández-Camacho 2001*

[d] *Gerber 2006*

[e] *Weighted average of birthrates reported in Gerber et al. 2010*

Results

The mean growth rate of the Los Islotes population calculated from the diffusion approximation of the data was $\mu_{obs} = 0.0592 \pm 0.236$ (mean ± SD). Mean growth rates calculated from diffusion approximations of each model were found to be significantly different (one-way ANOVA, unequal variances: $F_{5,55986.072} = 44565.48$, $P < 0.001$). All models except Models 2 and 4 were significantly different from each other (Games-Howell post hoc test: $\mu_{Model2} - \mu_{Model4} = 5.83 * 10^{-5}$, $P = 0.994$; all others: $P \leq 0.01$; Table 5). All model-predicted mean growth rates fall within the 95% confidence interval of the census data.

Comparing individual model projections to the census data resulted in significantly different SS scores (one-way ANOVA, unequal variances: $F_{5,55862.679} = 42538.50$, $P < 0.001$, Table 5) after taking the natural logarithm of the raw SS score. The demographic Models 1 and 3 received the lowest SS scores (2.232 and 2.242, respectively), where a lower SS score indicates a better fit to the data. These SS scores were significantly different from other methods of birthrate estimation (Games-Howell post hoc test: $P < 0.001$), but not from each other ($P = 0.372$). The RBA Models 2 and 4 showed a similar pattern (Games-Howell: $P = 0.876$ between Models 2 and 4, $P < 0.001$ for other models), though with higher SS scores than the demographic models (3.012 and 2.956, respectively). Model 6 (5.577) and Model 5 (16.226) followed with significantly higher SS scores than any other model (Games-Howell: $P < 0.001$ for both models). It should be noted that the log-transformed SS scores failed the Shapiro-Wilk test of normality,

though the large sample size should prove robust to this assumption of the one-way ANOVA.

By dividing the final abundance resulting from each model by the abundance observed at Los Islotes in 2008, I calculated the percentage of the final observed abundance projected by each model. This measurement resulted in significantly different mean abundance projections after a natural logarithm transformation (one-way ANOVA, unequal variances: $F_{5,55986.072} = 44565.48$, P < 0.001). The demographic models resulted in the lowest projected female abundance after 28 years (Model 1: 98.23%; Model 3: 99.24%), which were significantly different from each other and all other models (Games-Howell: P < 0.001). The RBA models overestimated female abundance by about 34% (Model 2: 134.62%; Model 4: 134.72%). Again, these models were significantly different than other models (Games-Howell: P < 0.001), but not from each other (P = 0.994). Models 5 and 6 also over projected female abundances (Model 5: 299.97%, Model 6: 180.45%), and were significantly different from the other models (Games-Howell: P < 0.001 for both models). Model results are summarized in Table 5.

Model sensitivity analysis

As is typical of long-lived, iteroparous animals, the highest elasticities were found in the juvenile and female survival parameters (Heppell *et al.* 2000). This was true of all models (Table 6). In the two-sex models, the parameter for male survival had negative elasticities for Models 3, 4, and 6 and a positive

elasticity in Model 5. Elasticity for K ranged between 0.458 and 0.670 for all

models. The elasticity of the birthrate parameter B was equal to 1.472 in Model 1

and 1.203 in Model 3. All other parameters were of low (<1) to moderate (<2)

elasticity.

Uncertainty in carrying capacity

To better understand the influence of uncertainty in the chosen K value, I

plotted the sum-of-squared differences of each model from the data evaluated

over a range of K values between 1 and 600 (Hilborn and Mangel 1997). I then

centered each plot at the best K estimate for each model (Fig. 4). From Figure 4,

the sum-of-squared differences of Models 1 and 3 are more robust to deviations

from their best estimates of K, followed by Model 4. In contrast, Model 5 is most

sensitive to these deviations.

Cost analysis

Gerber and her field team censused the Los Islotes population 10 times

over the month of July, 2004, for a total of 10 separate observations that required

6.38 hours in total. The effort resulting from this method of birthrate estimation

was therefore 0.00266 hr/obs/d. To observe male and female aggression, Gerber's

team spent a total of 11.33 hours in 11 days for a total of 224 observations,

resulting in an effort of 0.000192 hr/obs/d. To estimate male territory size, they

spent 88 hours in 11 days for 256 observations – an effort of 0.0313 hr/obs/d –

which brought the total effort of the RBA technique to 0.0315 hr/obs/d. From

Figure 5, the lower effort of the demographic estimate of birthrate also correlates

with lower SS scores. In general, I expect that as effort increases, there should be

a reduction in deviation from the census data. Because the RBA technique

required higher effort and resulted in larger errors, my results do not follow this

trend.

Table 5: Mean and standard deviation of model results from the diffusion approximation and comparison to census data. The SS score is the sum-of-squared deviations of each model from the data for each census year. Model projections of female abundance, given as percentages and mean projected abundance, are compared to observed abundances at Los Islotes in 2008 ($F_{2008,obs} = 203$). Effort of both demographic and behavioral methods of birthrate estimation is given as hours per individual observation per day. Bold values indicate models that are significantly different ($P > 0.05$) from all others.

Model	Diffusion Approximation μ (SD)	Comparison to Census Data			
		SS score (SD)	Percent Observed (SD)	Mean F_{2008} (SD)	Effort (h/obs/d)
1	**0.0464 (0.0106)**	2.232 (1.634)	**98.23 (30.08)%**	199.41 (61.07)	0.00266
2	0.0576 (0.0107)	3.012 (2.447)	134.62 (41.52)%	273.27 (84.29)	0.0315
3	**0.0468 (0.0107)**	2.242 (1.601)	**99.24 (30.40)%**	201.46 (61.71)	0.00266
4	0.0577 (0.0106)	2.956 (2.335)	134.72 (41.11)%	273.49 (83.46)	0.0315
5	**0.0865 (0.0098)**	**16.23 (7.619)**	**299.97 (84.76)%**	608.95 (172.07)	-
6	**0.0683 (0.0100)**	**5.577 (3.968)**	**180.45 (52.21)%**	366.32 (105.99)	-

Table 6: Elasticities for each parameter in all six models. The parameters include survival rates (S) of pups (P), juveniles (J), females (F), and males (M); juvenile growth rate (G); sex ratio (SR), carrying capacity (K); the demographic estimate of birthrate (B); and the observed aggression rates of females (A_F) and males (A_M), male territory size (Terr), and harem size (h).

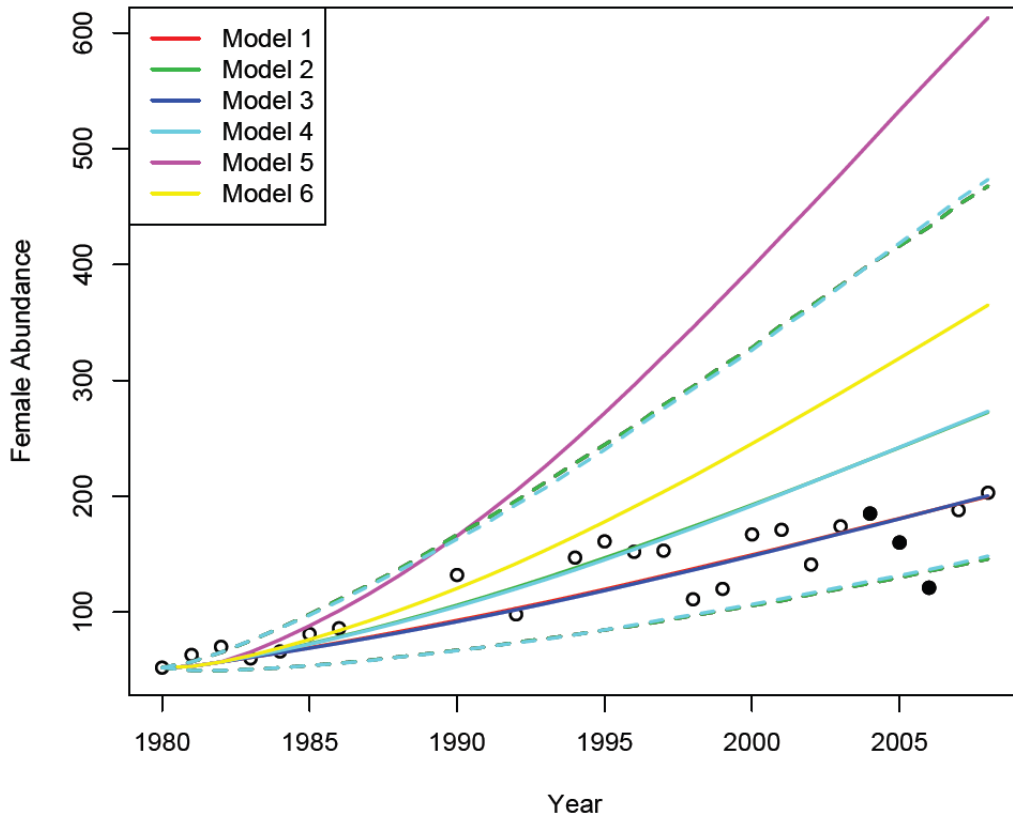| parameter	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
S_P	1.499	1.600	1.390	1.521	1.518	1.448
S_J	2.648	2.762	2.555	2.666	2.310	2.468
S_F	20.857	18.828	21.875	20.190	13.74	18.395
S_M	-	-	-0.490	-0.339	0.392	-0.428
G	1.693	1.783	1.606	1.768	1.658	1.821
SR	1.471	1.348	1.878	2.019	1.398	1.974
K	0.519	0.609	0.458	0.508	0.670	0.554
B	1.472	-	1.203	-	-	-
A_F	-	0.274	-	0.325	-	-
A_M	-	-0.918	-	-0.900	-	-
Terr	-	-0.148	-	-0.185	-	-
h	-	-	-	-	0.284	0.043

Figure 3: Projected female abundance of each model. Dotted lines indicate the 2.5[th] and 97.5[th] percentiles of populations projected from each RBA model. The lines of Models 1 and 3 and Models 2 and 4, respectively, lie on top of each other. Data points are observed abundances at Los Islotes in each census year, with filled points representing the years of double sampling for sea lion behavior and demographic counts for birthrate estimation.
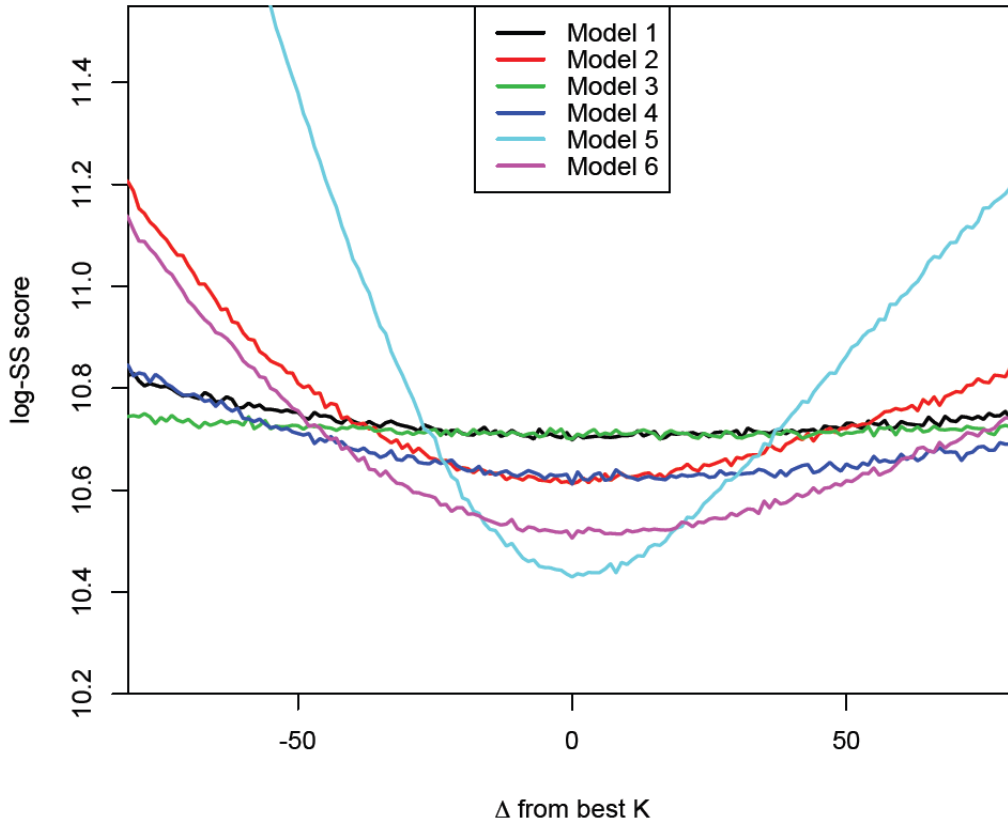
Figure 4: Goodness-of-fit plot of sum-of-squared deviations from the census data for each model at varying levels of K. The plots are centered on the best estimate of K for each model.
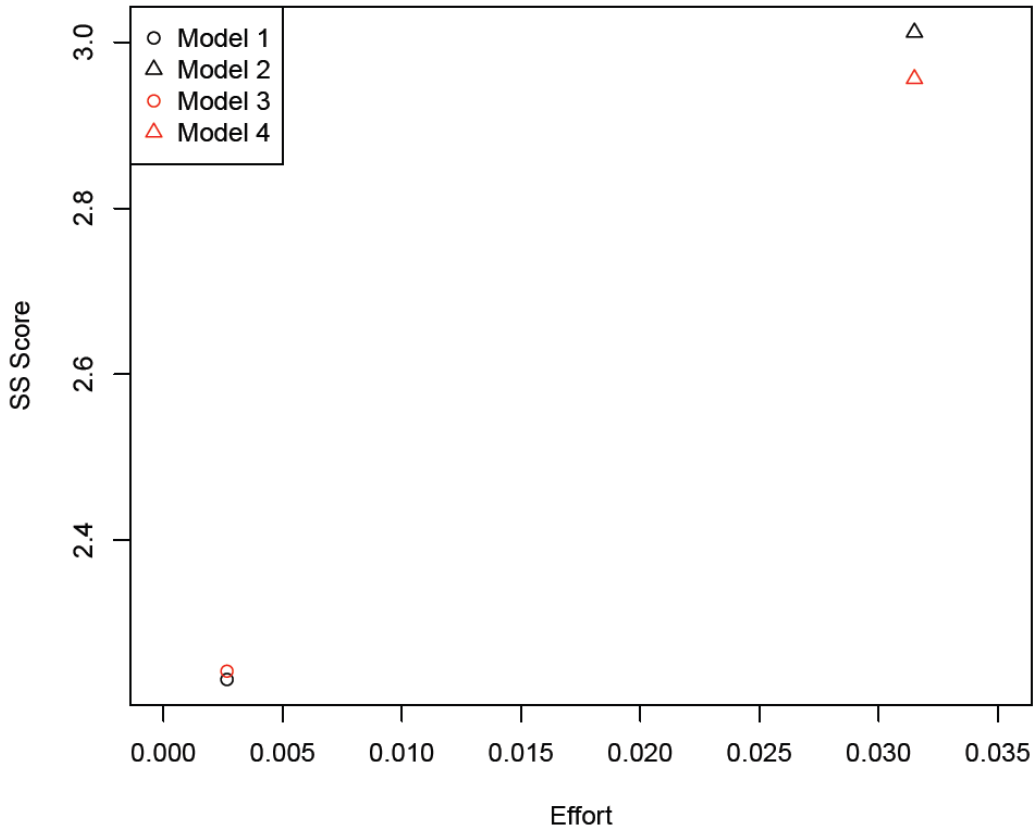
Figure 5: Cost analysis of models utilizing demographic (Model 1: black circle; Model 3: red circle) and RBA (Model 2: black triangle; Model 4: red triangle) methods of estimating birthrate. In both one- and two-sex formulations, the demographic model resulted in lower effort and error. The effort for a demographic estimate of birthrate was 0.00266 hr/obs/d (N = 10). Effort for birthrate estimation using RBA (0.0315 hr/obs/d) was calculated as the sum of aggression observation effort (0.000192 hr/obs/d, N = 224) and effort in estimating male territory size (0.0313 hr/obs/d, N = 256).

Discussion

As expected the demographic models performed best in all comparisons. This is largely because I chose to use the best estimate of carrying capacity, K, for demographic estimates of birthrate for other models within a comparison. In this sense, this pattern constitutes part of the design protocol for model comparison rather than a true result. It is more informative however to discuss the relative rank positions and projection differences of the other competing models in relation to the demographic models. I found that although estimating birthrate through rapid behavioral assessment does increase the error of a projected population, the amount of error may be acceptable. In each comparison, both RBA models projected female abundances that were more conservative than the harmonic and modified harmonic mean birth functions. This was true independent of model formulation (one- or two-sex, deterministic or stochastic). When considering final female abundances, Models 2 and 4 predicted values within 75 individuals of both demographic models and the census data. This estimation technique also retained to a large degree the robustness to uncertainty in carrying capacity shown in the demographic models, especially when the two-sex model formulation was used.

The same cannot be said of the theoretical birth functions. Model 5, which used the standard harmonic mean birth function, performed poorly in all areas of comparison, with the highest sum-of-squared deviations score. In Figure 4 this model is most sensitive to errors in carrying capacity estimation. Model 5 also overestimated final female abundance by almost 3 times the observed value.

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However the harmonic mean birth function modified for maximum numbers of offspring (Model 6) showed intermediate performance between the demographic estimate of birthrate and the standard harmonic mean birth function. Model 6 showed similar behavior to the demographic and RBA models in both comparison to data and sensitivity to errors in K. I therefore recommend that managers use this birth function when maximum offspring numbers are known, but data on birthrates are unavailable.

When considering the tradeoff between effort spent collecting data and model accuracy, effort and deviation from the census data are both lowest for the demographic models. Therefore these models are preferred. However, most of the effort in estimating birthrates through RBA resulted from collecting data on male territory size. This behavior has very little influence over birthrate estimation, though, because its covariate from the RBA regression is small (-0.001). I chose to use the regression equation with the most AICc support from the Gerber *et al*. (2010) study, but the next-best model did not include territory size. Perhaps using this second equation with only male and female aggression as covariates would result in a lower cost than traditional birthrate estimation.

Conclusions

My results suggest that RBA may be a viable method of monitoring this population in the future if observation costs can be reduced. To ensure the greatest accuracy in using this technique in this and other monitoring programs, I have developed a few guidelines for the use of RBA. First, the benefits of using RBA

will be overpowered when trying to use behaviors as indicators of highly sensitive demographic parameters. This is because the error introduced into the estimate through regression results in increasingly inaccurate population dynamics as the sensitivity of the parameter increases. I therefore suggest that the technique only be used on parameters known to have low or moderate sensitivities. For this same reason, RBA should only be used when the behavioral indicator explains a relatively large proportion of the variance in the demographic parameter.

Although I conclude that RBA may be beneficial to managers for this colony of California sea lions, I did not investigate how continued observation of sea lion behaviors may influence predictive ability. Future programs may benefit by updating population projections after repeated behavioral observations. This is evident in Figure 3, where the RBA model closely follows the trajectory of the population until the late 1990's. Reevaluation of the RBA model may therefore be necessary after about ten years in this system. I also did not explore how accurately this relationship between sea lion behavior and reproductive rates transfer to other colonies in the Gulf of California, especially to colonies with stable or declining populations. Future studies should investigate how transferable this technique is to other GoC colonies and other populations in North America, as behaviors vary across geographic ranges (Foster 1999). The wider the applicability of a behavioral indicator is, the more useful it will be to a variety of managers and biologists. However, because behavior tends to be taxon specific, application of this technique is most likely limited to within a population or species, or at most at the family level (Blumstein and Fernández-Juricic 2010).

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This work represents an important step in the inclusion of behavioral ecology in the field of conservation biology. Rapid behavioral assessment shows promise as an important management tool to increase the effectiveness of management decisions while reducing costs. I hope that this work inspires naturalists, conservation biologists, and wildlife managers to draw on their knowledge of animal behavior to benefit their work and the populations they monitor.

IV. GENERAL DISCUSSION

I have argued that conservation behavior can benefit by considering the interactions between behaviors and demography when making management decisions. This is due to the reciprocal relationship between many behaviors and demographic processes, though these relationships may be specific to the species in which they are observed. By including these relationships in population viability analysis, conservation behaviorists have the opportunity to contribute to a wide variety of wildlife management decisions and policies. This framework makes use of the quantitative nature of these population models to provide intuitive rules for the use of conservation behavior in management through decision analysis.

In particular, I have outlined three strategies that make use of the behavior-demography relationship. The first is the more familiar use of behavioral mechanisms in demographic models to increase biological realism and descriptive ability. Currently this strategy can be found in spatially-explicit models that include animal dispersal and habitat selection. The second strategy defines the relationship between a demographic process and a closely related behavioral index to approximate demographic rates for use in PVA. The third strategy uses well-understood behaviors as early warning flags of population decline.

The second strategy involves the proposed technique of rapid behavioral assessment, which uses a behavioral index as a proxy of a related demographic parameter. Once data have been collected on both the behavioral index and the traditional parameter, a regression can be used to translate future behavioral

observations into parameter estimates for PVA. Rapid behavioral assessment results in a tradeoff between model accuracy and program cost because this second-hand estimate increases observation error due to the variance around the RBA regression, but may greatly reduce the costs and effort surrounding estimation of the demographic parameter. If the error from RBA is small in relation to its program cost, repeated behavioral observations may be used to update PVA models for more efficient management decisions. I have provided a detailed example of this process in a breeding colony of California sea lions in the Gulf of California, Mexico.

This investigation resulted in four general guidelines for the use of RBA in population management: 1) The cost of observing the behaviors in the wild population must be less expensive than traditional methods of parameter estimation. 2) Behaviors closely related to the parameter of concern should be targeted as possible indices. These behaviors will generally stem from the natural history of the species in question. 3) The more precise the correlation between the behavioral index and the demographic parameter, the more applicable this tool will be. 4) RBA should only be applied to parameters that have low to moderate model elasticities, as the slight error from the RBA regression will be magnified by higher parameter elasticities.

Conclusions

This work demonstrates that conservation behavior focused on population biology has the ability to have wide-spread impacts on wildlife management. This

is because demographic models are increasingly implemented in conservation and management programs and behavior is intrinsically related to demography.

My approach in this study followed the advice of Caro (2007) in that I focused on the issues and outcomes that conservation biology is concerned with rather than trying to extend behavioral ecology knowledge to a conservation problem. Future conservation behavior research programs should focus on the general issues of saving money, improving the accuracy of limited biological information, and shortening the time needed to make informed management decisions. I hope that the framework outlined in this study provides structure to future conservation behavior programs.

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APPENDIX A

PERMISSIONS FROM CO-AUTHORS

APPENDIX A

Chapters II and III were coauthored with Leah R. Gerber and José Daniel Anadón
as independent studies for submission to separate academic journals. The
coauthors have given permission for the inclusion of these studies in this thesis.