



Stochastic simulation model for the Hawaiian monk seal
by Albert Lively Harting, Jr

A dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Biological Sciences
Montana State University
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Abstract:

The Hawaiian Monk Seal (*Monachus schauinslandi*) is an endangered marine mammal that lives almost exclusively in the remote Northwestern Hawaiian Islands. Recent trend estimates suggest that the species is declining in abundance due to a number of mortality sources, including starvation, intraspecific aggression, shark predation, and disease.

The primary objective of this project was to develop a comprehensive stochastic simulation model to aid in understanding how certain natural perturbations and management alternatives influence the monk seal population. The model uses the data on demographic rates, migration rates, and other life history components acquired through long-term investigations by the National Marine Fisheries Service. The model is specific to the life history of the monk seal, and was designed to be highly flexible so that a broad array of simulation scenarios could be structured.

The core sequence of steps in the model is survival (with options for multiple rate schedules and inter-atoll correlation in survival), reproduction, and migration. Each of these life history components is stochastically implemented, with the fate of individual seals determined by binomial sampling. All demographic parameters are specified as distributions, with simulation-specific values drawn from those distributions. Options available in the model include density dependent regulation, natural perturbations (shark predation, single or multiple male aggression, birth catastrophes, and survival catastrophes), and management intervention (removal of aggressive males, capture and captive rearing of females, translocation of females, and short-term captive maintenance of pups).

Trial simulations were performed to explore specific phenomena and demonstrate the power of the model. The simulations indicated that age structure anomalies would likely lead to further decline at French Frigate Shoals over at least the next 10-12 years. This atoll was largely insensitive to management intervention targeted at improving pup survival because poor survival of juveniles negated the positive effects of those actions. Density dependent regulation acted to homogenize simulation trajectories, often masking the effects of other perturbations. Uncertainty regarding the correct form of density dependence in the monk seal makes long-term projections (> 25 years) tenuous until those uncertainties are resolved. The expected outcomes from natural or management-induced perturbations are best explored through shorter-term projections in which various different density dependence modes are employed.

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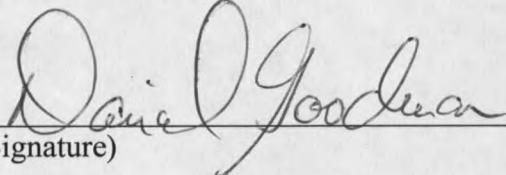
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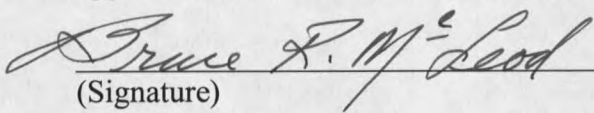
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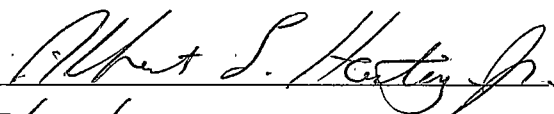
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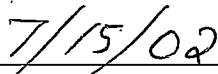
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ABSTRACT

The Hawaiian Monk Seal (*Monachus schauinslandi*) is an endangered marine mammal that lives almost exclusively in the remote Northwestern Hawaiian Islands. Recent trend estimates suggest that the species is declining in abundance due to a number of mortality sources, including starvation, intraspecific aggression, shark predation, and disease.

The primary objective of this project was to develop a comprehensive stochastic simulation model to aid in understanding how certain natural perturbations and management alternatives influence the monk seal population. The model uses the data on demographic rates, migration rates, and other life history components acquired through long-term investigations by the National Marine Fisheries Service. The model is specific to the life history of the monk seal, and was designed to be highly flexible so that a broad array of simulation scenarios could be structured.

The core sequence of steps in the model is survival (with options for multiple rate schedules and inter-atoll correlation in survival), reproduction, and migration. Each of these life history components is stochastically implemented, with the fate of individual seals determined by binomial sampling. All demographic parameters are specified as distributions, with simulation-specific values drawn from those distributions. Options available in the model include density dependent regulation, natural perturbations (shark predation, single or multiple male aggression, birth catastrophes, and survival catastrophes), and management intervention (removal of aggressive males, capture and captive rearing of females, translocation of females, and short-term captive maintenance of pups).

Trial simulations were performed to explore specific phenomena and demonstrate the power of the model. The simulations indicated that age structure anomalies would likely lead to further decline at French Frigate Shoals over at least the next 10-12 years. This atoll was largely insensitive to management intervention targeted at improving pup survival because poor survival of juveniles negated the positive effects of those actions. Density dependent regulation acted to homogenize simulation trajectories, often masking the effects of other perturbations. Uncertainty regarding the correct form of density dependence in the monk seal makes long-term projections (> 25 years) tenuous until those uncertainties are resolved. The expected outcomes from natural or management-induced perturbations are best explored through shorter-term projections in which various different density dependence modes are employed.

INTRODUCTION

Background on the Hawaiian Monk Seal

The Hawaiian monk seal (*Monachus schauinslandi*) is an endangered marine mammal that now occurs almost exclusively in the remote Northwestern Hawaiian Islands. It is one of only two mammals endemic to the Hawaiian Islands, and is classified both as *depleted* under provisions of the Marine Mammal Protection Act, and *endangered* under the Endangered Species Act of 1973.

Recent trend estimates for the species are not encouraging, due largely to a steady decline in seal abundance at the largest, and formerly most productive, of the breeding atolls¹ (Craig and Ragen 1999; Ragen and Lavigne 1999). The best estimates of current status place the number of monk seals at less than 1500, with the vast majority of the population breeding on only six atolls (Figure 1). Causes implicated in the decline are varied. Historically, killing by humans for pelts and food led to substantial mortality (Ragen 1999; Ragen and Lavigne 1999). While anthropogenic mortality remains a concern (Gerrodette and Gilmartin 1990), natural mortality sources appear to be responsible for the more recent declines. These include starvation (Craig and Ragen 1999), intraspecific aggression (Hiruki, Gilmartin, *et al.* 1993, Starfield *et al.* 1995), shark predation (Hiruki, Gilmartin, *et al.* 1993, Alcorn and Kam 1986, Hawn 2000), and disease (Banish and Gilmartin 1992).

¹ Although not all of the breeding sites are technically "atolls," the terms atoll, island, and subpopulation will be used interchangeably throughout this document to refer to the main breeding locations.

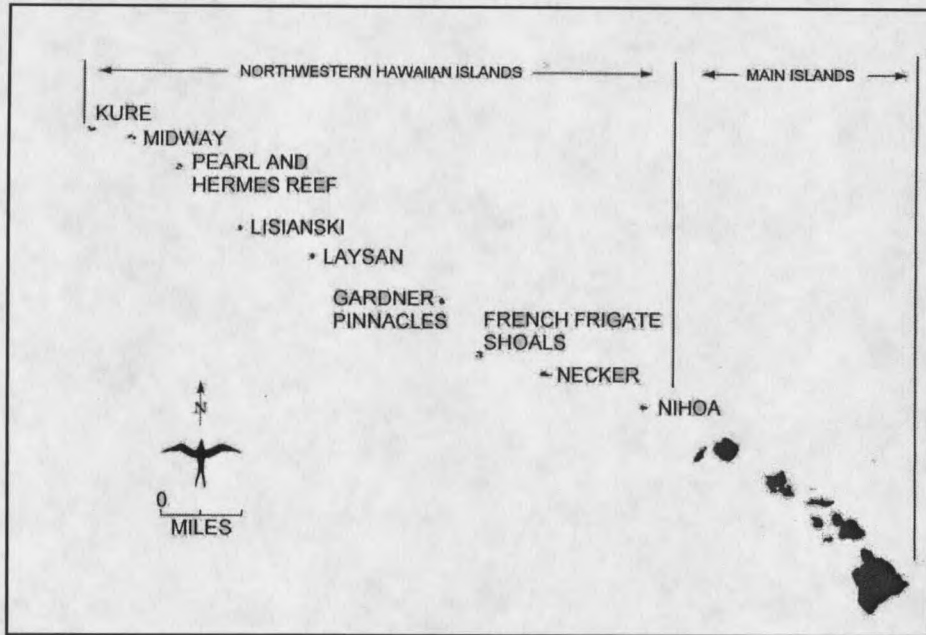
The National Marine Fisheries Service (*NMFS*) is the lead agency charged with the management and recovery of the monk seal. The long-term dataset for guiding the recovery of the monk seal is relatively rich, especially as compared to that available for many other endangered species. Counts of monk seals have been made since the late 1950s, although census methods for the early counts were variable and did not encompass the whole of the breeding range (Kenyon and Rice 1959; Rice 1960; Ragen and Lavigne, 1999). Since 1983, *NMFS* has conducted systematic monitoring of monk seal populations at all of the main breeding locations. Data are collected on total numbers, age/sex composition, reproductive rates, physical characteristics of newborns, mortality sources, and other key data.

This wealth of data has made possible the development of a sophisticated, species-specific, stochastic simulation model for the Hawaiian monk seal. The model integrates all of the available information on demographic rates, metapopulation dynamics, and life history of the monk seal, and provides managers with a powerful instrument for evaluating the expected effects of natural or management-induced perturbations.

This paper describes the structure of the simulation model, the methodology for generating the parameters required as input by the model, and the strategies for handling uncertainties in the requisite data. Results from a set of simulations are presented to demonstrate the power of the model for simulating specific scenarios, and testing the sensitivity of the trajectories to manipulation of vital rates. Special consideration will be

given to issues that bear on the reliability of the monk seal model (and stochastic simulation models in general) in long-term population projections and risk assessment.

Figure 1. Map of the Northwestern Hawaiian Islands



Primary Objectives for the Project

The primary objective of this project was to develop a comprehensive simulation model to serve as an exploratory tool for assessing the consequences of management strategies and natural perturbations. As a secondary objective, we wished to use the model for predicting future abundance and quasi-extinction risks (Ginzburg *et al.* 1990) for the monk seal. The latter objective falls within the broad umbrella of population viability analysis, or PVA.

These two objectives are complementary, but distinct. The salient question is whether accomplishing the first (development of the model) necessarily enables the second. That is, if the best possible simulation model is coupled with the best available data, will it be sufficiently reliable to conduct the long-range projections required for PVA? In this light, the requirements for proper PVA will be considered in some detail in a subsequent section.

Why a Species-Specific Simulation Model?

Recently, a number of sophisticated generic simulation models have been made available for use in PVA and other management applications. These include RAMAS (Akçakaya 1994), INMAT (Mills and Smouse 1994), VORTEX (Lacy 1993), GAPPS (Harris *et al.* 1986), and others. While these programs are generally designed to be flexible and adaptable to a wide range of life histories (Mills *et al.* 1996; Brook *et al.* 2000), none have the specificity to attend to all of the nuances of the ecological system in which the monk seal resides.

For example, properly simulating the dynamics of the shark predation scenario at French Frigate Shoals requires steps that deal with the probability of predation on a subset of pups born at the atoll, a probability for management "detection" of the predation event, and another probability governing the likelihood of management removal after detection. No generic model is capable of correctly capturing all components of this predation scenario. Eliminating any of these steps from the model would result in either an overly simplistic representation of the predation event, or would

obscure key aspects of the predation event that we might wish to explore. This observation accords with other studies that found that packaged software failed to capture known aspects of a species' life history (e.g., Haig *et al.* 1993; Brook *et al.* 1997). Since the life history component of a model constitutes the mechanistic framework within which demographic processes operate, using a model that merely *approximates* a species' true life history renders model outcomes highly suspect.

One of the problems associated with the use of packaged PVA software is the tendency for misinterpretation of the results when all of the limitations and assumptions inherent to the model are not explicitly considered. Even when the limitations are recognized, it is tempting to treat the results of simulation exercises as qualitatively reliable (Haig *et al.* 1993; Reed *et al.* 2002). This may be a faulty assumption, since seemingly minor disparities in model design or input can lead to markedly different results (Mills *et al.* 1996; Brook *et al.* 1997). In any simulation exercise, but especially when using packaged software, the user must be aware that the software is providing a simple answer to a specific question: that which is formulated in the specified scenario, as constrained by the design and limitations of the given model (Caughley 1994). The "answer" that emerges from a set of simulations must be considered in light of both the question and the limitations of the model. Building a model explicit to the monk seal circumvents some of this problem since all aspects of the model's design are explicitly known and are available for modification if, upon further reflection, it is determined that they do not properly represent the monk seal's life history.

Another justification for undertaking a species-specific model is the allowance for further refinement as new issues emerge or as our knowledge of the monk seal's life history expands. Boyce (1993) stresses that modeling should be an ongoing enterprise, by which the model's design is iteratively improved to reflect our enhanced understanding of the species and its habitat. He likens this process of ongoing model refinement to the concept of adaptive management (Walters 1986), with a dynamic link between research, management and model validation.

Building a simulation model specific to the monk seal also provides indirect heuristic benefits that would not accrue from use of packaged software. Model building provides a framework for formulating relevant questions, examining the data in novel ways, and synthesizing all that we know (or don't know) about the species (Boyce 1992, 1993; Akçakaya and Burgman 1995; Beissinger and Westphal 1998). As expressed by Akçakaya and Burgman (1995: page 706):

“... (T)here is very significant value in building a model for its own sake. It clarifies assumptions, integrates knowledge from all available sources, and forces biologists to be explicit and rigorous in their reasoning. ... It results in a set of logical statements that are internally consistent and allows us to explore the consequences of what we believe to be true, even in the absence of relevant data.”

Designing a comprehensive model requires us to confront those areas where our understanding is deficient and, hopefully, to devise strategies for rectifying those deficiencies. Beissinger and Westphal (1998: page 836) elaborated further on this point:

“What demographic models can highlight is the uncertainty behind decision making in terms of how little we often know about population processes of paramount conservation importance or how ignorant we are about which management strategies will work best.”

While generating reliable predictions is the *raison d'être* of model building, placing too much emphasis on “statistically feeble” predictions (Boyce 1993) may cause the heuristic benefits of modeling to go unrecognized, and may promote the use of poor predictions.

Salient Issues in Simulation Modeling and Population Viability Analysis

The secondary objective of the project was to determine if the monk seal simulation model was sufficiently comprehensive and reliable to conduct formal PVA. As defined by Boyce (1992, 1993), PVA entails “evaluations of data and models for a population to anticipate the likelihood that a population will persist for some arbitrarily chosen time into the future.” Since this concept was first formalized by Shaffer (1981) and later Gilpin and Soule (1986), it has been variously celebrated and maligned. Proponents maintain that PVA is the least subjective way to evaluate extinction risks and classify populations according to those risks (e.g., Lindenmeyer *et al.* 1993; Ruggiero *et al.* 1994; Brook *et al.* 2000; Brook *et al.* 2002; Clark *et al.* 1991; Mace and Lande 1991; Possingham *et al.* 1993). Skeptics counter that proper PVA is rarely possible due to data limitations and/or the dynamic nature of ecological systems (e.g., Caughley 1994; Taylor 1995; Beissinger and Westphal 1998; Coulson *et al.* 2001). The criticisms have not always been restrained. The results of PVA have been viewed as “pseudoscientific estimates of extinction” (Beissinger and Westphal 1998), that “exaggerate our capabilities and carry a high risk of failure” (Ludwig 1999), and (endowed as they are with a quantitative façade) convey a “fallacy of illusory precision” (Reed *et al.* 1998).

Given the disparate views on the merits of PVA, it is worthwhile to review the key points tendered by both camps, and consider how the current project fits within the debate. It should be noted that many elements of this debate apply not just to PVA models, but also to stochastic modeling in general. Key issues that encumber PVA attempts will be considered, particularly those that relate to the monk seal data and the modeling exercise at hand. Foremost among these issues is the proper handling of uncertainties in simulation modeling, and means for coping with density dependent variation in demographic rates.

Overview of PVA

The objectives for undertaking PVA are varied, but may include predicting the future size of a population, estimating the extinction (or quasi-extinction) probability over time, assessing the influence of certain management strategies, and exploring the consequences of different assumptions on population dynamics (Coulson *et al.* 2001; Ralls and Taylor 1997). PVA has been applied to diverse taxa, among them the grizzly bear (Shaffer 1983; Shaffer and Samson 1985), the spotted owl (Marcot and Holthausen 1987), red-cockaded woodpeckers (Haig *et al.* 1993), forest primates (Kinnaird and O'Brien 1991), manatees (Marmontel *et al.* 1997), and many others.

For proper PVA, it is necessary to select, or construct, a model that captures the salient aspects of a species life history, and use the model to quantify the probability of extinction within a specified number of years. PVA models can assume many forms, from quantitatively rigorous models with challenging mathematics (e.g., Goodman 2002), to much simpler qualitative models (Ruggiero *et al.* 1994). Most PVA models emphasize

demographic and/or genetic components of risk (Boyce 1992; Goodman 1987, 2002), although PVA can be approached from an ecological perspective as well (Harcourt 1995).

Regardless of the type of model, PVA must be comprehensive in that it takes full advantage of all available data and considers all of the important dynamical processes that bear on the long-term persistence of the population. Goodman (2002) emphasizes that for proper PVA, the model must take into account not only everything that is *known* about the dynamics of the populations, but also everything that is *not known*. The latter requirement alludes to the fact that wherever there is uncertainty in the effect of a factor on the dynamics of the population, that uncertainty must be explicitly quantified and propagated through the analysis.

Formal PVA is essentially a form of *risk analysis*, in which the likelihood of future events is evaluated probabilistically according to the starting conditions and their associated uncertainties (Goodman 2002; Burgman *et al.* 1993). Consistent with this framework, certain conventions have emerged regarding the time frame and probabilistic threshold for evaluating PVA results. For example, among the earliest (and still oft cited) PVA efforts was Shaffer's grizzly bear model, in which he suggested that a 95% probability of persistence over 100 years was a suitable criterion to evaluate extinction risks for most large mammals (Shaffer 1981, 1987; Shaffer and Samson 1985). Similarly, Mace and Lande (1991) proposed that the IUCN adopt a definition for an "endangered" species as one having a 20% probability of extinction within 20 years or ten generations (whichever was greater).

