The Spotted Owl

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Introduction

A key purpose of *The UMAP Journal* is to provide significant examples of mathematical modeling, presented in a classroom context, that illustrate how mathematics is used as a tool to understand a problem and guide management towards a solution. A major contemporary concern that gives rise to management problems is the welfare of wildlife populations.

There is a general fear that perhaps a quarter of the earth's current plant and animal species will be extinct by the end of the century, primarily as a result of human activity. In this process the world will likely lose about half of its primate species, along with several of the larger mammals and birds. Concern over this rapid rate of species loss and the consequences of massive extinctions at the hand of humans has led to the emergence of a new field of science, conservation biology [Dobson 1988]: At the center of a current controversy on the Pacific Coast of the US is the northern subspecies of the spotted owl.

The National Forest Management Act of 1976 legislates that timber harvesting on National Forest lands must be managed so that viable populations of native vertebrate species are maintained over a wide domain. Home range territory for a nesting pair of spotted owls consists of a huge tract ranging from 2,000 to 4,200 acres of mature and old-growth forest, usually exceeding 200 years in age. The Forest Service management plan calls for 500-600 spotted owl habitat areas (SOHAs), each containing 1,000 to 3,000 acres of suitable habitat per nesting pair. This management plan is at the center of a heated controversy between the timber industry and environmental organizations.

The timber industry claims that management for the spotted owl is too costly. Simple arithmetic suffices to underscore the economic impact. The profit from harvesting an acre of old-growth forest is more than $4,000. Now 550 SOHAs at (conservatively) 1,000 acres each, if not tied up in spotted owl habitat, would yield about $2.2 billion in profit for the timber industry. In general, the value of timber set aside to accommodate a single nesting pair is about $8 million. Accordingly, cynics refer to the spotted owl as the "snail darter of the 1990s" (in reference to a small fish whose endangerment temporarily halted the construction of the Tellico Dam in Tennessee in the early 1970s). To emphasize the magnitude of the economics, about 44% of Oregon's economy and 28% of Washington's depend on national forest resources [Forest Service 1988].

Environmentalists claim that continued logging of mature and old-growth forests will drive the owl to extinction. The spotted owl population is currently estimated to contain only 1,500 pairs of owls. Logging the old-growth habitat can destroy the population. In British Columbia, logging has virtually eliminated suitable owl habitat and only 7 pairs are known to exist in the entire province.

Passions run high, since each side in the controversy views the other as the enemy. Many in the timber industry believe the spotted owl is expendable by virture of its impact on jobs and local economies. Environmentalists feel logging of old growth should stop completely in order to preserve necessary owl habitat. A coalition of conservation groups has filed a petition with the US government for endangered species status for the owl in Oregon's coastal range and Washington's Olympic Peninsula, with threatened status throughout the rest of the owl's range. In such fashion battle lines are now drawn.

The ultimate goal of conservation management is to designate appropriate reserves that function to conserve a whole ecosystem, such as an old-growth forest ecosystem. The dynamics of such an ecosystem are far too complex to model. Usually attention is focused on maintaining a viable population of a specific species that requires a large area of habitat. The welfare of this designated species is thought to indicate the general state of the ecosystem taken as a whole, hence it is called an "indicator species." The spotted owl, acting as the indicator species for the Pacific Northwest old-growth coniferous forest ecosystem, is perched at the center of attention and controversy.

An inaugural "Special Section" of the noted journal *Ecology* was devoted to the spotted owl [Simberloff 1987, Dixon and Juelson 1987, Salwasser 1987]. We especially recommend Simberloff [1987], who commented

> All of this information has been made available to modelers whose efforts, though frankly preliminary, have indicated some key factors in the vicissitudes of owl populations, and at least as importantly, have suggested what new biological information is needed for accurate prediction.

This article is devoted to an introduction to such models.

Background Assumptions

The basic biology of the spotted owl leads to an initial choice for a model. First, the owl is a pulse breeder, with a short breeding season in late April to early May. Accordingly, we adopt a discrete model to project the population from year to year. Second, the field ecologist can distinguish three stages in the life history of the owl: juvenile (first year), subadult (second year), and adult (third year and beyond). Hence, we construct a discrete model based on these three stages of the owl's life.

To formulate our first model, we keep things simple. We want to capture the general demographics, not the microscopic details. The rationale here is that if we can't solve the easy problem, we won't solve the hard problem. The modeling process will act like a zoom lens, in which we first develop the general at-a-distance picture, then focus on the important details.

Accordingly we hold all demographic parameters constant, initially ignoring population effects due to environmental fluctuations. We first need to get a feel for how the owl population changes on its own, before studying effects on that change due to environmental variation or human perturbations such as habitat removal due to logging. Further, we construct a model only for the female population, justified primarily by a one-to-one sex ratio and by the fact that limits to the population's potential for growth are determined by female survivorship and fecundity.

Model Terms

In order to facilitate formulation of our first model, we introduce the following notation and terms:

t time in years

J_t juvenile population at time t

S_t subadult population at time t

A_t adult population at time t

s_J annual juvenile survivorship (proportion of juveniles alive at time t who survive to become adults at time $t + 1$)

s_S annual subadult survivorship

s_A annual adult survivorship

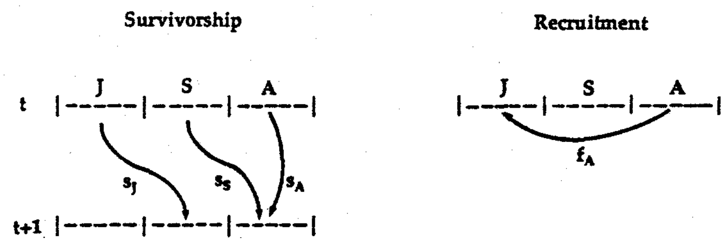

Figure 1 Demographic diagram for a model of the spotted owl population distinguishing juvenile (J), subadult (S), and adult (A) stages. a. Survival proportions for each stage from one year to the next. b. Recruitment of juveniles in pulse breeding, with census immediately after the birth pulse.

f_A fecundity (average number of juveniles produced by an adult female each year)

Model Formulation

In accordance with the given background, assumptions, and terms, we formulate a model for a pulse-breeding female population whose adult fecundity and survivorship are *nonsenescent* (independent of age).

The model must capture the key features of population demographics: survivorship and recruitment; i.e., how the owl survives and reproduces, as depicted in Figure 1.

We can now formulate a mathematical model by translating these aspects of survivorship and recruitment (the demographic parameters) into equations:

$$\begin{aligned} J_t &= f_A A_t \\ S_{t+1} &= s_J J_t \\ A_{t+1} &= s_S S_t + s_A A_t. \end{aligned}$$

Model Analysis

The system of equations can be condensed into a single equation by noting that

$$\begin{aligned} A_{t+2} &= s_S S_{t+1} + s_A A_{t+1} \\ &= s_S(s_J J_t) + s_A A_{t+1} \\ &= s_S s_J(f_A A_t) + s_A A_{t+1}. \end{aligned}$$

Hence the dynamics of the system can be monitored by the adult population, in the form

$$A_{t+2} - s_A A_{t+1} - s_J s_S f_A A_t = 0.$$

This is a second-order linear difference equation with constant coefficients (see Sherbert [1980, 21-29] for methods of solution). Such an equation has a long-term solution of the form $A_t = c\lambda^t$, where c is a constant and λ is the larger root of the equation

$$x^2 - s_A x - s_J s_S f_A = 0.$$

The quadratic formula gives

$$\lambda = \frac{s_A + \sqrt{s_A{}^2 + 4 s_J s_S f_A}}{2}.$$

The same conclusion can be reached by rewriting the system of equations as

$$\begin{aligned} J_{t+1} &= \qquad\quad s_S f_A S_t \;\; + s_A a A_t \\ S_{t+1} &= s_J J_t \\ A_{t+1} &= \qquad\quad s_S S_t \quad\;\; + s_A A_t, \end{aligned}$$

thereby generating the stage matrix model

$$n_{t+1} = M n_t,$$

where

$$n_t = \begin{bmatrix} J_t \\ S_t \\ A_t \end{bmatrix}$$

is the stage cohort vector at time t and

$$M = \begin{bmatrix} 0 & s_S f_A & s f_A \\ s_J & 0 & 0 \\ 0 & s_S & s_A \end{bmatrix}$$

is the stage projection matrix. The characteristic equation for M is the quadratic equation above, and the dominant eigenvalue of M is λ.

Model Interpretation

The number λ has a significant ecological interpretation, since λ acts as a measure of the overall rate of change of the population. In particular,

- if $\lambda > 1$, the population is increasing;
- if $\lambda = 1$, the population is steady;
- if $\lambda < 1$, the population is declining.

Hence, from a wildlife management perspective, in order to determine the status of the population, estimate λ. Among ecologists λ is known as the *rate of increase* of the population.

The value of λ is critically dependent upon the survival and fecundity estimates. At this time there is some debate among ecologists about these values, which has led to different estimates of λ (Table 1). A statistical analysis with accompanying confidence intervals for λ yields no further insight, as the intervals straddle the critical value of 1.

Our first model is fruitful in that it uses key demographic parameters to identify an indicator λ that acts as a population "weather vane." Based on current knowledge, however, as Table 1 indicates, our perception of the value of λ is too fuzzy. In order to zoom in for a closer view, we need to do some fine tuning.

The fine tuning must be done on two levels. First, on the ecological level, we need improved field data. Since research money for data collection is limited, and collecting data on spotted owls is expensive and difficult work-the owl is nocturnal, lives in rugged and remote old-growth forests, nests high in tall trees and snags, and has a low density--careful thought must be given to what data are to be collected. In particular, the focus has to be on improving estimates on the demographic parameters to which λ is most sensitive.

Table 1.
Estimates of model parameters.

Parameter	US Forest Service [1988]	Lande [1988]
s_J	0.34	0.11
s_S	0.97	0.71
s_A	0.97	0.94
f_A	0.24	0.24
λ	1.046	0.96

Second, on the model level, we need to enhance our original simple model by incorporating further considerations that have a strong influence on λ. For this endeavor, it is important that modelers and ecologists talk to each other. A modeler acting in isolation may incorporate a parameter that cannot be measured in the field in a practical manner (e.g., age of an adult bird); such a modeling endeavor usually results in a solution in search of a problem. Candidates for model refinement include the following:

- *Age at first reproduction.* Ecologists have noted that a two-year-old owl (age at first breeding) may have a depressed fecundity.
- *Reproductive senescence.* Does longevity affect λ?
- *Environmental stochasticity.* Is λ sensitive to statistical variation of the demographic parameters in the model? Environmental fluctuations can have a major influence on extinction probability, especially for small populations.
- *Density dependence.* Does either crowding or very wide dispersal affect survivorship or fecundity?
- *Habitat fragmentation.* What is the effect of logging on the owl population? Does habitat need to be contiguous over a wide area to facilitate a threshold level for successful juvenile dispersion?

Other considerations are the effects of genetics, catastrophes (most notably forest fires), prey abundance, competition (intrusion by barred owls), and carrying capacity (resource limitation).

Model Enhancement

Once a litany of options is developed, model enhancement can proceed rapidly. For example, a cadre of eager students with computers can quickly produce a multitude of stochastic simulations. Stochastic versions of our simple model produce lively classroom activity and yield insights into the type of fine tuning needed by resource management.

We illustrate the process of model enhancement by consideration of the age of first reproduction: Are two-year-old owls less fecund than older owls? We begin by incorporating into the model a separate category T for two-year-old owls, letting

T_t be the population of two-year-olds at time t,

A_t be the population at time t of adults more than two years old (so we have redefined the meaning of A),

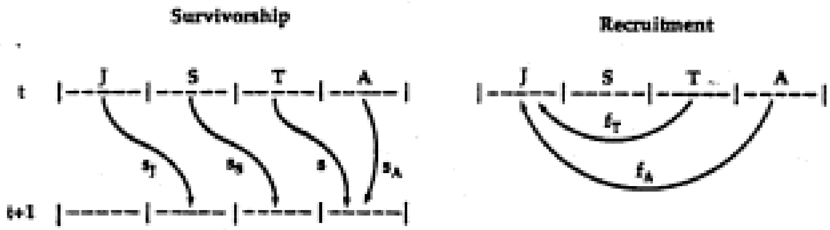

Figure 2. Demographic diagram for a model of the spotted owl population that distinguishes fecundity of two-year-old owls (category ***T***). a. Survival proportions for each stage from one year to the next. b. Recruitment of juveniles in pulse breeding, with census immediately after the birth pulse; $0 \le f_T \le f_A$.

f_T be the fecundity of two-year-old owls, and

f_A. be the fecundity of owls more than two years old.

We summarize the situation in **Figure 2**.

Our diagram leads to the model equations

$$\begin{aligned} J_t &= f_A A_t + f_T T_t \\ S_{t+1} &= s_J J_t \\ T_{t+1} &= s_S S_t \\ A_{t+1} &= s_A T_t + s_A A_t . \end{aligned}$$

After some substitutions and algebraic simplifications, we can convert this system to a single equivalent equation in terms of the adult population:

$$A_{t+3} - s_A A_{t+2} - s_J s_S f_A A_{t+1} + s_J s_S s_A (f_A - f_T) A_t = 0,$$

which has corresponding characteristic polynomial

$$p(x) = x^3 - s_A x^2 - s_J s_S f_A x + s_J s_S s_A (f_A - f_T).$$

As before, the wildlife manager's key concern is whether or not the largest root λ is greater than 1. Note that

$$\lambda \geq 1 \iff p(1) \leq 0$$

$$\iff 1 - s_A - s_J s_S f_A + s_J s_S s_A (f_A - f_T) \le 0$$
$$\iff 1 \le s_A + s_J s_S f_A - s_J s_S s_A (f_A - f_T).$$

Examining the last expression suggests that the parameter with by far the most influence on λ. is s_A, adult survivorship, especially since the owls have a high adult survivorship (around 0.95). In fact, a 50% drop in s_J, s_S, f_T, or f_A will not have the effect of a 10% drop in s_A! Even in a worst-case scenario of $f_T = 0$, the decrease in λ is only about 0.01.

Using the same approach in our simpler model quickly yields that

$$\lambda \ge 1 \iff 1 \le s_A + s_J s_S f_T,$$

with the same observations about the dominant influence of adult survivorship.

This initial exploration of model enhancement suggests that the modeler and the field ecologist should focus greater attention on the factors that affect adult survivorship. We direct the interested reader to the literature for further enhancements.

Epilogue

The problem of statistical design lies much deeper than mere determination of sample size to obtain some suitable confidence interval for λ. Frequently the resource manager must simply live with whatever data happen to be available. The problem is how to use λ in the decision-making process; in statistical terminology, the question is how to view the null hypothesis.

The timber industry views the problem as

$$H_0: \lambda \ge 1 \text{ vs. } H_a: \lambda < 1,$$

while an ecologist concerned about the owl as a threatened or endangered species views the problem as

$$H_0: \lambda < 1 \text{ vs. } H_a: \lambda \ge 1.$$

The struggle over which of these two views will prevail as public policy is currently the subject of dramatic courtroom battles and intricate legal maneuvering.

We emphasize that it is possible for a population in demographic equilibrium (λ =1) to decline if its suitable habitat is also declining. The spotted owl, strongly associated with mature and old-growth forests, is experiencing such a decline in its preferred habitat.

Resource modelers and managers are now being asked by government and business to determine to what extent a wildlife population can be reduced in abundance and still maintain its viability as a species. Such questions challenge the very soul of a nation. We must come to grips with the value of species, genetic diversity, and preservation of life forms while simultaneously considering the economic welfare of people dependent on resource industries. The very notion that we are trying to determine minimum viable population as a management option is an indication of the nature and extent of the controversy. Mathematical models will play an increasingly important role as our society struggles to make informed choices regarding its place amid the other residents of Planet Earth.

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