Matrix Population Models as a Tool in Development of Habitat Models

Gregory D. Hayward and David B. McDonald[1]

Abstract.—Building sophisticated habitat models for conservation of owls must stem from an understanding of the relative quality of habitats at a variety of geographic and temporal scales. Developing these models requires knowing the relationship between habitat conditions and owl performance. What measure should be used to compare the quality of habitats? Matrix population models represent a powerful tool to aid in designing habitat research. Through sensitivity and elasticity analysis we can identify the demographic transitions most important in determining population growth. Matrix methods also provide a powerful method for assessing individual fitness in varying environmental conditions. Matrix models can help us decide how to: (1) focus field efforts toward measuring the most important demographic parameters, and (2) focus on those habitat characteristics with the greatest effect on population dynamics.

Models of owl habitat relationships rely on information describing the association between owl species and measurable habitat characteristics. An ideal habitat model will rank the relative quality of habitats at one or more spatial and temporal scales. Developing such a ranking system requires evaluation of the performance of individuals or populations in a variety of habitats. Designing such studies is not trivial (e.g., see review in Morrison *et al.* 1992). Along with the problems of sampling owl performance at the appropriate range of temporal and spatial scales, and of replicating samples, a measure of 'performance' must be chosen. What metric measure should be used to compare the quality of habitats?

Biologists studying habitat associations of various vertebrate taxa employ a wide range of metrics. Relative comparisons of habitat use vs. availability of habitat are common (see examples in Alldredge and Ratti 1986). In other studies population density, reproductive rate, measures of body condition, or less frequently, survival rates are used to compare habitats (e.g., Morrison *et al.* 1992, VanHorne 1983). The choice of metrics is often determined largely by logistical and sampling constraints. We suspect, however, that the choice of metrics is often made without rigorous consideration of the relative value of different measures of performance. Some biologists contend that comparison of individual fitness among habitats would provide the ideal metric to ultimately rank habitat quality.

We propose that measures derived from population matrix models (Caswell 1989, McDonald and Caswell 1993) provide flexible, powerful and intuitively appealing metrics with rigorous links to fundamental theory in population ecology and genetics. The metrics include many of those listed above, including measures of individual fitness (McGraw and Caswell 1996) and population growth. They also include rigorous sensitivity analyses that point to the most critical life history transitions and allow comparison among populations or habitats that vary in one or more important ways. The models readily incorporate stochastic features and density dependence, and are especially useful when data are incomplete. Much of the output is robust to non-equilibrium conditions and populations can be classified by age or stage (e.g., breeder versus floater) to incorporate the most biologically meaningful aspects of the life history. The methods therefore provide an important tool to guide future efforts in research and management.

[1] Assistant Professor of Wildlife Ecology and Assistant Professor of Ecology, respectively, Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071

DESCRIPTION OF THE BASIC MODELING FRAMEWORK

Matrix population models can classify life cycles either by age or stage. Age-classified models examine population dynamics by dividing the continuous age variable into discrete age classes, each of the same duration. Stage-classified models are more flexible, and accommodate analysis of more complex life cycle patterns. The stages may describe social status (e.g., breeder versus floater), developmental stages, or spatial locations (e.g., high-quality versus low-quality territory). Transitions among the stages are governed by **vital rates** that describe processes such as growth, fertility, survival or even the probability of becoming a breeder or obtaining a high-quality territory.

Matrix population models were initially developed by Leslie (1945, 1948). Caswell (1989) provided a comprehensive and synthetic overview of the modeling framework, and McDonald and Caswell (1993) provided a briefer review of their application to avian studies. Matrix models are the basis for several computer packages for population and viability analysis (e.g., RAMAS). As a supplement to the computer-based matrix analyses, life cycle graphs provide a powerful and intuitively appealing tool for model development. We begin with a brief introduction to age- and stage-classified models and then provide an example to illustrate its application to questions related to the habitat, conservation, and population dynamics of owls.

Age-classified Models

Age-classified models place estimates of fertility and survival rates in a square 'projection matrix'. In the simplest case (Leslie matrix) the top row of the projection matrix represents age-specific fertility, while the subdiagonal represents age-specific survival. A common extension is to add an element at the lower right that represents survival of 'adults' (the term in fig. 1). The remaining elements of the projection matrix are zero.

The corresponding life cycle graph (fig. 2) is mathematically equivalent to the matrix but provides a more intuitively appealing version of the life cycle. In the life cycle graph, circles (called **nodes**) represent stages or states. Arrows (called arcs or loops) connecting the

(a)

$$\begin{bmatrix} F_1 & F_2 & F_3 \\ G_{21} & & \\ G_{31} & P_2 & P_3 \end{bmatrix}$$

(b)

$$\begin{bmatrix} .04 & .31 & .53 \\ .20 & & \\ .03 & .46 & .46 \end{bmatrix}$$

Figure 1.—*(a) A Leslie matrix with three age classes—first-year birds, second-year birds, and 'adults'. The P_x represent survival rates from one age class to the next. F_x represents the fertility of females at age x, and is a compound term given by the product of the number of offspring, M_x, and the survival of females from the post-breeding census to the next breeding pulse (P_x). If we conducted a pre-breeding census, the parameterization would be slightly different (see McDonald and Caswell 1993). For most bird studies it is more convenient to conduct post-breeding censuses, using the number of fledglings as the count for 'first-year' birds.*

(b) A numerical example of using the matrix in figure 1a to 'project' the population at time t + 1 ('projected' census vectors to the right of the equal sign) from the population at time t (census vector to the right of the matrix). At time t there were 52 first-year owls (fledglings), 16 second-year birds (just past their first birthday) and 32 'adults'. At time t + 1 we therefore expect 55 fledglings, 17 second-year birds, and 34 'adults'. The population growth rate, λ, for this example is 1.06.

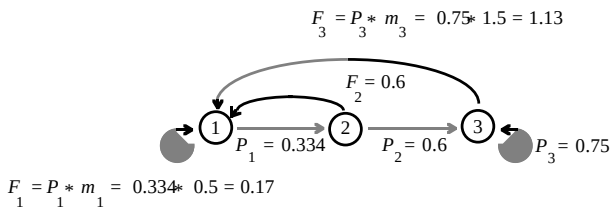

Figure 2.—*A life cycle graph corresponding to the Leslie matrix given in figure 1a. The circles (nodes) represent the three age classes, while the arrows (arcs) represent the vital rates—survival and fertility, as given in figures 1a and 1b. The self-loop on Node 3 (P_3 = 0.75) represents the survival rate of 'adult' females. For more complex life cycles, the graph is very useful in formulating the model from which a matrix can be constructed for computer analysis.*

nodes represent the vital rates (transitions between states). In figure 2, Nodes 1 and 2 represent first-year and second-year individuals, respectively, while Node 3 represents 'adult' individuals. Parameter estimates for transition rates are represented by P_x — indicating survival rate from stage or age class x to $x + 1$, and F_x — indicating the mean number of female offspring produced by females of age x, m_x, times the probability, P_x, that a female of age class x (censused just after the breeding season) will survive from that census until the next breeding pulse, just before the annual census. 'Adult' survival is represented by an arc called a 'self-loop', P_3, that represents the (survival) probability of returning to the 'adult' stage at the next census.

From this simple representation of the population vital rates we can calculate a number of useful demographic parameters (table 1). Figure 1b shows hypothetical values for the matrix

Table 1.—*Demographic metrics obtained from analysis of a population matrix, **A**, with elements a_{ij} representing the transitions from st(age) j to (st)age i.*

Parameter	Derivation	Importance
Growth rate (λ)	Dominant eigenvalue of **A**	Finite rate of increase; can be developed as measure of individual fitness.
Sensitivity (s_{ij})	$\partial\lambda/\partial a_{ij}$ (partial derivative of λ with respect to a_{ij})	Sensitivity of λ to a change in a one of the vital rates (a_{ij}); directly equivalent to a selection gradient in quantitative genetics.
Elasticity (e_{ij})	$s_{ij} * a_{ij}/\lambda$	Proportional sensitivity of λ to a change in one of the a_{ij}.
Stable (st)age distribution	Right eigenvector	Proportion of population in each (st)age.
Reproductive value	Left eigenvector	Value of an individual of a given (st)age as a seed for population growth.
Cohort generation time (μ_1)	(Caswell & McDonald 1993)	Mean age of reproduction for a cohort.
Age of stage	(Cochran & Ellner 1992)	Mean and variance for age of individuals in a given stage. (used for stage-classified models)
Damping ratio	Second eigenvalue of **A**	Measures rate at which damped oscillations return the population to equilibrium.

elements and 'projects' the expected census vector at time $t + 1$ from the census at time t. Because λ (=1.06) is slightly greater than one, the number of individuals at time $t + 1$ is slightly greater than at time t. Important assumptions underlying the simple Leslie matrix model are absence of density dependence and constancy of the age-specific vital rates.

Age-classified models have several limitations. For long-lived organisms, matrix truncation or the adult survival self-loop (fig. 2) may affect some aspects of the results (see McDonald and Caswell 1993, p. 166). For example, senescence is not well modeled by either abrupt truncation or a self-loop for 'adult' survival. Although senescence has long been ignored as a demographic feature of avian populations, recent analyses indicate that it may be an important feature of avian population dynamics (McDonald *et al*. 1996). A more important drawback of simple age-classified models is that age may not be the most appropriate basis for assessing population dynamics. For example, individuals of the same age that differ in reproductive status (e.g., breeders versus floaters) will have very different demographic outputs. Such life cycles are better analyzed with stage-classified models that capture the most biologically important transitions.

Formulating a Stage-classified Model

Stage structured models overcome some of the shortcomings of the age-classified models. In particular, complex social dynamics or breeding systems can be modeled and analyzed with these models. Caswell (1989) and McDonald and Caswell (1993) describe formulation and analysis of stage-classified models and provide examples for taxa with a variety of life cycles. As a first step in formulating a stage-classified model, the life cycle graph is particularly important and useful.

We illustrate the development of a stage-classified model by describing one possible life cycle graph (fig. 3) for the dynamics of a Boreal Owl (*Aegolius funereus*) population in which some proportion of the population experiences delayed reproduction. The stages in the life cycle are: Node 1—first year birds, Node 2—second-year birds that did not breed as first-year birds, and Node 3—'experienced or older' breeders. As is often the case in population models, we assume female demographic dominance (we therefore model only the female

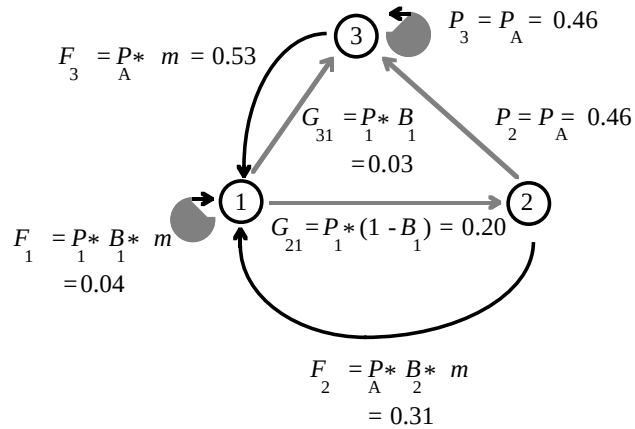

Figure 3.—*A life cycle graph for a population of Boreal Owls. Node 1 represents first-year birds, Node 2 represents second-year birds that did not breed in their first year, and Node 3 represents a mixture of experienced breeder second-year birds and birds in their third year or beyond. The arcs (transitions) between Nodes 1 and 3, and between Nodes 1 and 2 are labeled G_{ij} because they are compound terms involving the probability of becoming a breeder at age x, denoted B_x.*

segment of the monogamous population). We parameterized the life cycle based, in part, on data collected for a Boreal Owl population in the wilderness of central Idaho (Hayward *et al*. 1993).

Parameterization for this stage-classified life cycle is somewhat more complicated than for a simple Leslie matrix, mostly because we are introducing a new transition parameter—the probability of becoming a breeder. Transitions therefore exist whose critical aspect is not changing age but the change from non-breeding to breeding status. We used the following estimates for the vital rates: first-year survival, $P_1 = 0.23$, 'adult' survival, $P_A = 0.46$, and $m = 1.16$ female fledglings per female. We assumed a 15 percent probability of reproduction by first-year birds (B_1), 65 percent by second-year birds, and 100 percent by all older birds. The 65 percent second-year breeding percentage points to a potential pitfall in parameterization. Remember that some (15 percent) of the first-year breeders become 'experienced' breeders and move directly to Node 3. The proportion of birds that breed in their second year but <u>not</u> in their first year, B_2, is therefore 0.588 (0.15 + 0.588 ∗ (1 - 0.15) = 0.65 overall). Note also that Node 3 will be

heterogeneous for age—a few second-year and third year birds that first bred from Node 1 or 2 (shown by reproductive arcs going back to Node 1), a few third-year first-time breeders (via the arc from Node 2 to Node 3 describing individuals that were not in the proportion B_2 that first bred in their second year) and returning experienced breeders, represented by the self-loop on Node 3.

In the life cycle we have formulated in figure 3, individuals can move to stages other than the next numerical stage. We therefore need a double subscript for transitions among stages. We specify such transitions among stages with the notation G_{ij}, where the transition is to Node i from Node j. For example, because the probability of breeding for first-year birds in Node 1, B_1, is 0.15, $G_{31} = P_1 * B_1 = 0.23 * 0.15 = 0.0345$. Note also that we must specify that individuals moving to Node 2 were yearling non-breeders by adding the term $1 - B_1$ (the probability of <u>not</u> breeding as yearlings). The additional 'change of status' elements, B_x and $1 - B_x$, represent the most significant difference between the formulation for an age-classified versus a stage-classified model. Other possible stage classification terms could include greater age-specificity incorporated in additional nodes, parameters describing growth (e.g., for life cycles where size is more important than age in determining survival or fertility) or nodes describing territory quality (the arcs would then describe the probability of obtaining high versus low quality territories). The possibilities are limited only by our ability to estimate important transitions in the life cycle.

ANALYSIS OF THE MODEL

The parameter estimates for vital rates (transitions) in the life cycle graph are converted to the equivalent matrix formulation (fig. 4), and then analyzed using standard matrix techniques. Although the calculations can be made rather easily employing widely available software, we emphasize the importance of correctly formulating the life cycle graph and its constituent transition values. It is difficult to obtain reliable estimates of stage specific survival and reproduction—misformulation of the life cycle graph will lead to incorrect conclusions. Time spent on carefully formulating the life cycle graph to account completely for all possible transitions is negligible compared to the field effort necessary to collect accurate data—but it is equally essential.

(a)

$$\begin{bmatrix} F_1 & F_2 & F_3 \\ P_1 & & \\ & P_2 & P_3 \end{bmatrix}$$

(b)

$$\begin{bmatrix} 0.2 & 0.6 & 1.1 \\ 0.3 & & \\ & 0.6 & 0.8 \end{bmatrix} * \begin{bmatrix} 52 \\ 16 \\ 32 \end{bmatrix} = \begin{bmatrix} 55 \\ 17 \\ 34 \end{bmatrix}$$

Figure 4.—*(a) Matrix corresponding to the life cycle graph in figure 3.*
(b) Matrix of numeric values corresponding to the graph in figure 3.

Given a correctly formulated life cycle graph and its corresponding matrix, we can assess important parameters of the population dynamics. Caswell (1989) and McDonald and Caswell (1993) describe methods to calculate the demographic metrics given in table 1. In the context of providing input for studies of habitat associations, sensitivity analysis and the measurement of individual fitness are arguably the most important metrics.

Demographic Sensitivity, Elasticity and Fitness Analysis

Demographic sensitivity means the sensitivity of λ (population growth) to changes in particular demographic rates. Sensitivity measures the impact on λ of changing the <u>absolute</u> magnitude of a particular vital rate (say second-year survival) relative to changing other vital rates. An extension of the sensitivity analysis is elasticity analysis, which assesses the <u>proportional</u> sensitivity of λ to change in a vital rate. Both sensitivity and elasticity are useful measures. One advantage of elasticities is that they are weighted by the magnitude of the original arc in the life cycle. Thus, arcs of very low magnitude tend to yield lower elasticities, even if they are quite sensitive. For example, λ might be very sensitive to a change in the probability of breeding as a yearling. If, however, that is a

very rare event (say only 1 percent of owls breed as yearlings), and is unlikely to respond to changing management practices, we might be better guided by elasticities which will emphasize vital rates that are of large current magnitude and that may be more responsive to changes in management. A second advantage of elasticities is that they sum to 1.0, providing a straight forward basis for comparing elasticities across varied life histories.

Eigenvalue analysis of the projection matrix yields the elasticities and sensitivities. McDonald and Caswell (1993) provide an accessible explanation of the necessary calculations. Kroon *et al*. (1986) also discuss the uses and computation of elasticities. The computations can be performed most easily by employing software designed for matrix algebra (e.g., Mathematica, MathCad, RAMAS).

Elasticity analysis of our example life cycle for boreal owls (fig. 3) indicates that survival of breeding adults is by far the most important transition (fig. 5). Only two other transitions stand out: reproduction by adults and the transition from breeding as yearlings to becoming 'experienced' breeders. We can also calculate the mean age of the experienced and older breeders in Node 3 ($\bar{x}$ = 4.3 ± 3.0) as developed by Cochran and Ellner (1992) and other metrics outlined in table 1.

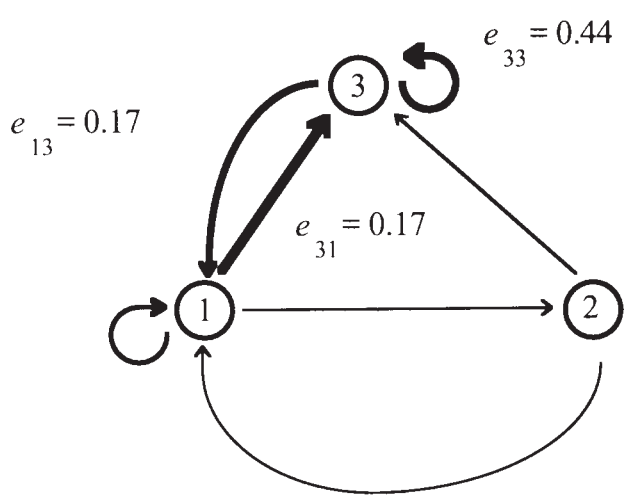

Figure 5.—*Life cycle graph corresponding to the Boreal Owl data shown in figures 3 and 4. Values represent elasticities for the three most important transitions in the life cycle.*

In a few cases, data may be sufficient to compute fitnesses directly for different habitats—possibly the ideal case for habitat analyses. McGraw and Caswell (1996) show that with data on lifetime reproduction and age at death, one can calculate an individual's 'population growth rate', λ, that serves as an integrated measure of fitness. They also show that even where data are incomplete, powerful analyses are possible. The technique is straightforward—the fitnesses are computed from the dominant eigenvalue of the reproductive outputs (half the offspring production, because our analyses are restricted to females) in the top row and survival values of 1.0 in the subdiagonal, with the dimensionality of the matrix equaling the life span of the individual. McGraw and Caswell (1996) provide examples from two long-term avian studies. By calculating a set of individual fitnesses across different habitats, one could directly assess the fitness consequences due to the habitat differences.

USING THE RESULTS FROM AN ELASTICITY ANALYSIS

Matrix models can be a powerful supplement to developing owl habitat models in at least two ways. First, it can provide the focus for gathering field demographic data. Second, it can highlight the most important life cycle transition for the species, and thereby guide the development of models customized to address the habitat variables most important to the population dynamics. We briefly discuss both of these.

Understanding the Life Cycle

A matrix model can help focus our field efforts. For example, our boreal owl model suggested that 'adult' survival was of overwhelming importance. The results suggest that field effort devoted to greater understanding of both variation in survival and the factors affecting survival would be particularly useful. Studies of clutch size, fledging success and other facets of reproduction, on the contrary, may be less worthy of intensive effort. The model can also guide the development of habitat models by ensuring that they incorporate the critical transitions in life cycle. The results of our Boreal Owl model suggests that any habitat model will need to incorporate features that affect 'adult' survival. This should, for example, emphasize studies on winter habitat and roosting site requirements.

Identifying Key Habitat

Building a sound conservation strategy for a species demands an understanding of the effect of habitat change on important demographic processes. Many studies of habitat relationships examine differences in used and available habitat, avoiding the question of how habitat characteristics are linked to demographic performance. It is not always possible to measure demographic performance in different habitats. However, when we do measure demographic performance as a metric to gage habitat quality, what metric should be used to compare the quality of habitats?

Matrix modeling provides a powerful tool to help focus habitat studies. Through elasticity analysis we can identify the demographic transitions most important in determining population growth. We can then design habitat studies that focus on the habitat elements most important to sensitive or elastic stages of the life history. We thereby provide a strong link between demography and habitat characteristics. By measuring the more 'important' vital rates in conjunction with our studies of habitat characteristics, we can rank habitats, in terms of quality, based on a defensible metric. In some cases we may even have the luxury of directly comparing individual fitness across different habitat types.

Insights from elasticity analysis can also help us identify WHAT habitat characteristics to measure. For instance, if elasticity suggests that adult survival is an important transition, and natural history observations indicate that predation is an important form of mortality for adults, our focus in habitat studies might change. Consider the potential difference in focus if we stress measures of reproduction (clutch size, fledging success) in a cavity nesting owl versus survival of adults. Management may focus on snag management in one case and characteristics related to predator risk for adults in the other. Elasticity analysis, then, may help us identify key groups of habitat variables to quantify during our studies of habitat associations. Without the insights provided by matrix analysis, we might have overlooked these habitat characteristics.

CONCLUSIONS

Matrix population models can help us; (1) determine what demographic characteristics to measure during our studies of habitat associations, and (2) focus on the habitat characteristics that have the greatest impact on population growth. Matrix models therefore represent an important tool in the design and implementation of owl habitat studies.

We caution, however, that applying matrix models to improve the design of habitat studies should not lead us to approach our work with tunnel vision. Although, matrix methods can point toward critical portions of a life cycle, we should not lose sight of the importance of other transitions. Reproduction by young birds may dominate an elasticity matrix, suggesting the importance of breeding habitat. However, this does not indicate that successful management can neglect habitat that is important for other life cycle functions. Obviously, if all the potential nest sites are gone, it doesn't matter how insensitive one was to changes in reproductive transitions. Instead, the matrix results indicate where the greatest gains may be realized in focused habitat improvement efforts.

For many biologists one of the greatest benefits of matrix modeling may come in the process of building the life cycle graph based on the life history data they have for their species. Building the graph can highlight the complexity of possible transitions and identify field data requirements.

The paucity of data on survival and reproduction may represent a barrier to application of matrix models in owl research and management. However, the ease of applying these models provides the opportunity to use them even in the face of sparse demographic data. We can learn from matrix models by exploring the behavior of the model given different assumptions regarding the vital rates of our target population. Therefore, we don't need perfect estimates of vital rates. We suggest playing WHAT-IF GAMES by observing the behavior of the elasticity matrix under a range of plausible vital rates. Frequently, analysis under assumptions that span the range of plausible values will lead to similar results, consistently identifying the same group of important transitions.

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