Study Guide for Conceptual Models

Summary

1. Describing and examining your internal conceptual models of a species or particular ecology increases understanding of the conclusions you reach on the status and baseline of listed resources, the expected exposure and responses to an action's stressors and subsidies, and the risk posed to the listed resources.
2. There are several ways to describe and illustrate your internal models.
3. These models provide the framework of your arguments.
4. The analytical framework itself is a conceptual model framework for the overall consultation analysis.

Introduction

Central to achieving our goals of robust, transparent, replicable, understandable and well-defended analyses and documents is the creation and use of explicit frameworks. Building upon the age-old themes of showing your logic train, putting your brain on paper, and stating your assumptions, this module describes and explores some of the common tools we use, or can use, to both understand and describe the effects of actions on species and critical habitats. These tools often form the foundation of the arguments we present during discussions, in our analyses and in consultation documents. The use of conceptual models and images provides a clear identification of the underlying data and assumptions we are using in our analyses. These models also allow for discussion between parties to evaluate, revise, and refine the models. Note: the term "model" is used often in this document. Do not assume that this refers only to quantitative or computer models. Many of the examples in this guide may include numbers for illustrative purposes, but you can create and use robust qualitative models as well. Bear in mind that when this guide indicates that we would need to establish that some response or risk occurs, it does not mean that we have completed a quantitative analysis – instead (and most frequently) we have presented a compelling case that it is reasonable to expect that the result occurs or is likely to occur.

We can create models describing:

- the life cycle of the species,
- the population structure and dynamics of the species,
- the resources the species depend upon, and
- the relationship of these resources with various components of the species' life cycle.

These models provide a basis for our exposure, response, and risk analyses. These models are also persistent in that they can be used for all consultations on the species and do not need to be recreated for each consultation unless we gain new knowledge. This provides for replicability between consultations and gives biologists, action agencies, and applicants common footing for the analysis.

In addition to these types of conceptual models, we can also create models of the analyses themselves. For example, we can establish the details of our analytical approach and describe:

- the types of questions we will ask,
- the information needed and how we will gather the data,

- how we will proceed in the face of uncertainty,
- how we will establish whether resources are exposed to the stressors of an action,
- how we will determine the response of listed resources to those stressors,
- the scenarios we will evaluate to determine the risk posed by the action, and
- how we will determine whether the action is likely to jeopardize the continued existence of the species or result in the destruction or adverse modification of critical habitat.

Models

What is a model? Models generally are an abstraction or simplification of reality. They are tools used to explore and understand processes or systems we cannot directly or easily manipulate. They are also a tool to answer questions about possible outcomes resulting from different treatments. Creating models can be enlightening because the process reveals what we do and do not know about connections and causalities. The creation of a model should also result in explicit delineation and explanation of key assumptions and data.

Unconsciously, we use conceptual models all of the time. Without conceptual frameworks of how a system works, we might spend all of our time trying to figure out how to survive. For example, to start a car we know that you put the key into the ignition, turn the key in a clockwise direction, and push down on the gas pedal with your foot. Our internal model tells us that when we turn the key, the battery will supply power to the starter to turn the engine and to the sparkplugs to initate ignition, and that when we press the gas pedal gasoline will be supplied to the combustion chambers where the sparkplugs will ignite it and the engine will then start. This seems simple enough, but to someone who has never driven before, understands the basics of a combustion engine, or even seen a car, it is completely mysterious. We sense this same mystery when we turn the key, press the gas pedal, and nothing happens. Some hidden assumption in our internal model has been violated (no gas, battery is dead, starter is broken, etc.). It is the same with the natural systems and species that you may deal with on a daily basis. You may use your internal model of the system or species in your discussions and writings, but the listener or reader cannot follow along if they do not have the same internal model. If we do not detail our model, along with its hidden assumptions, it is difficult for the reader to understand and diagnose existing or potential problems in the system.

Putting the model down in words or images allows us to share this internal model with others and also tests our own knowledge or assumptions about the system. While thinking of the "start the car" scenario above, your internal model may be more of a muscle memory than actual words in your head. That is, you may not understand anything about the inner workings of an engine, just that when you turn the key and press the gas, the car starts. Writing the model down on paper so that another person could start the car highlights unconscious details, assumptions made, and requires conscious examination of connections and relationships.

In ecology, conceptual models generally describe how a system, species, or process is believed to function, how it has been altered, and how actions might change conditions. Conceptual models express ideas about components and processes deemed important in a system, document assumptions about how components and processes are related, and identify gaps in knowledge – they are working hypotheses about system form and function (Manley *et al.* 2000). Quantitative models, such as those run on your computer, have a conceptual model at their heart. Numbers and equations have been determined via observation and experimentation, extrapolation, inference, or assumptions for each portion and linkage in the conceptual model.

Why do we need to be explicit about our internal models? There are many reasons, including both internal and external pressures to provide understandable, transparent and defensible decisions in endangered species management. From the simplest perspective, we need to define and explain our models so that non-biologists can understand the information we request during consultations and the use to which we put that information. Following on the car analogy above, you will get resistance when you ask for gasoline if people don't understand why or what you need it for. Detailing the model and all of the connections within the model may also reveal assumptions that you did not realize you were making. Those assumptions can now be tested and verified or changed as necessary to comport with the best available information.

We are also under daily pressure to use “sound science” and often quantitative science. We cannot meet this latter challenge for all species, but using the models described in this guide as well as others found in the ecological literature provides a strong foundation for the qualitative assessments we can conduct. Quantitative models are not necessarily better than qualitative ones. As mentioned above, most quantitative models actually have a conceptual model skeleton. Depending on the strength of the numbers and equations used in the quantitative model, the results may be no more predictive than a qualitative analysis using the same skeleton. Avoid the temptation to treat quantitative model results as “true” (and watch for this tendency in others as well). The results of a quantitative or qualitative model are only “true” for the tiny world of the model itself. Applying model results to the real world requires careful assessment of how the model reality matches actual reality, how the model takes variance into account, and whether the model answers the question posed.

Use in Analyses

In section 7 consultations, we commonly, albeit unconsciously, use conceptual models to understand species and habitat. These models are used in all facets of the consultation, from determining whether individuals will be exposed to an action, to determining their likely response, to evaluating the risk the action poses to the probability of survival and recovery of the species.

For the species, we have models of population function and structure, species’ life cycle, and biological and ecological requirements - which lead to habitat models. For habitats, we recognize how the ecosystem works or how it should work and the pathways and causal linkages (physical, chemical, biotic) by which species gain the resources they need.

As mentioned above, these models live on from consultation to consultation, whether they are explicit or not. Therefore, the models can be articulated prior to or unconnected with any particular consultation. The model can then be reviewed and verified. Once established, the models can be used by all parties to a consultation. As needed, various portions of the model can be expanded upon to meet the needs of the consultation or tailored to the affected population or ecosystem, but the starting framework should be the same to ensure consistency between consultations.

Species Models

The BIDE factors and age/sex structure. It may seem obvious that one of the internal calculations we are running during a consultation is whether the amount of lethal take that a project is likely to cause exceeds the ability of the population to absorb it, but this is not always explicitly stated in the consultation documents. One of the simplest and yet most powerful models of a species is a calculation of how populations persist or decline over time. Populations grow and decline through four fundamental processes: birth, immigration, death, and emigration, commonly referenced as the BIDE factors. Population size as a result of the BIDE factors can be expressed as an equation:

$$N_{t+1} = N_t + \text{Births} + \text{Immigration} - \text{Deaths} - \text{Emigration}$$

This equation reads as: the numbers at time t+1 (N_{t+1}) are determined by the numbers at time t (N_t) plus the numbers of births and immigrants and minus the numbers of deaths and emigrants that occur during that time interval. If births and immigration are greater than deaths and emigration, then the population will grow. If it is the opposite, the population will decline. For a consultation, it may not be necessary to have specific numbers to complete this formula, but an understanding of the relationship between the different BIDE factors for your particular population or species can be very illuminating during the risk analysis. For example, a population may have a low birth rate, but immigration levels high enough to adequately sustain the population at current numbers (a sink population). The effects of an action that disrupts the breeding cycle for one year will have different consequences for this population than an action that prevents migration into the population (see Box 1 for an example).

Of course, a simple application of the BIDE equation assumes that a population is uniform in that all individuals are contributing equally. But a population is really made up of several age classes and (usually) different sexes. The effective/active population size may be significantly smaller. For example, the total population may be fairly large, but if there has been low recruitment for several years, the population may be poised to suffer sharp declines and the effective (reproducing) population may actually be much smaller than the total population.

A good example of this type of population is the razorback sucker (*Xyrauchen texanus*) population in Lake Mohave, on the lower Colorado River. Although spawning has been documented, few larvae are surviving to reach reproductive age due to predation by nonnative fish. The population is made up almost exclusively of older, senescent adults (USFWS 2002). This information is valuable in consultation. The impact of a project may be much more significant when it is targeted at a particular age class or sex than if we assume the impact is felt equally over the whole population. Consider the risk posed to the species from an action that kills pre-reproductive or reproductive individuals versus one that kills older, senescent adults.

For the razorback sucker example, an age structure diagram would be useful to demonstrate the ratio of the various age classes in a population at a given time. This is particularly useful to document if exposure to a stressor from the project may affect one particular age class versus another.

Age structure diagrams are fairly easy to interpret. A broad base and pinched top suggest a young population with a potential for rapid population growth (depending on the survival rates between age classes) (Figure 1). If the diagram is bowed out in the middle, this may imply a strong cohort at reproductive age, but little recruitment is occurring (Figure 2). As this population ages, the diagram may begin to look “wasp-waisted” (Figure 3). Over the long term, population growth may be slowed, or even decline; in other instances, this structure explains the weak and strong cohorts seen in some species.

Sex ratio models are useful in a similar way, particularly if the project may affect one sex more than the other. Along with the age structure diagram, these diagrams also help you get a true grasp of the effective population size. The two diagrams are often combined as in the examples below; see Figure 4 for an example of an imbalanced or skewed sex ratio. Based on the example in Figure 4, some factor is preferentially killing females. As a result, future reproduction and overall population sizes are likely to decline significantly. It can be quite illuminating to compare the age and sex structures of the current population against the structures the population should have based on the species’ unperturbed life history.

Figure 1

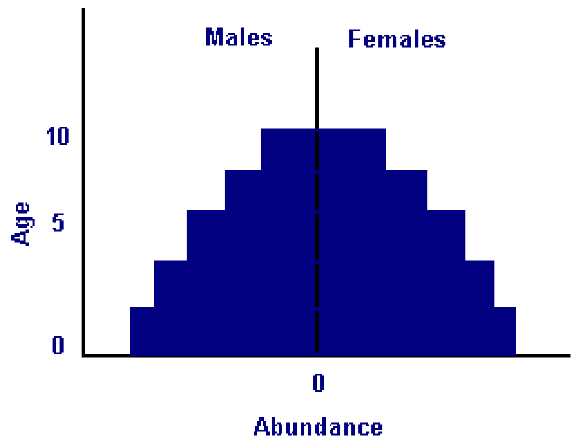


Figure 2

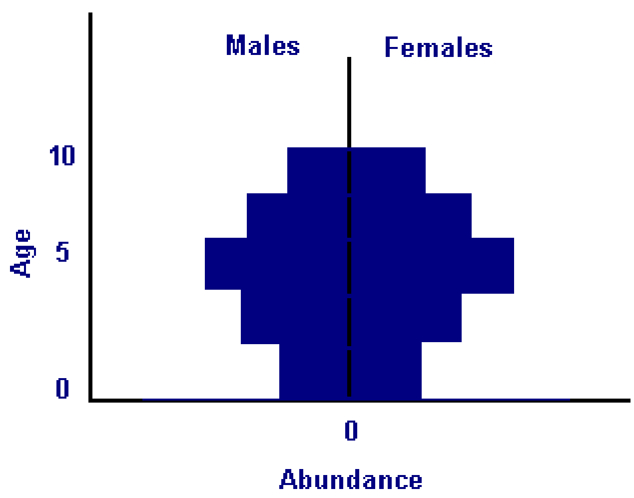


Figure 3

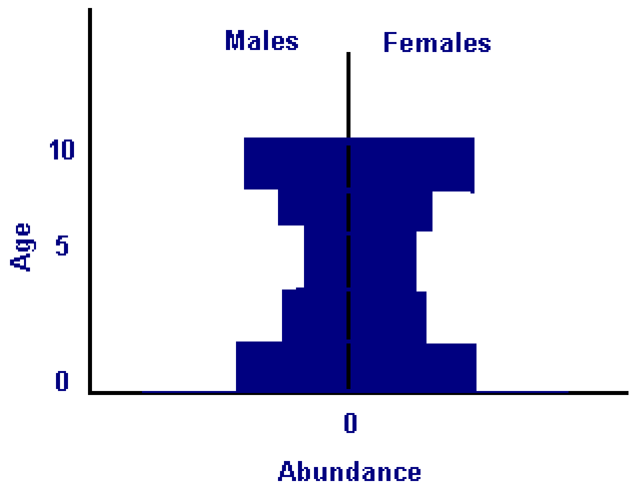
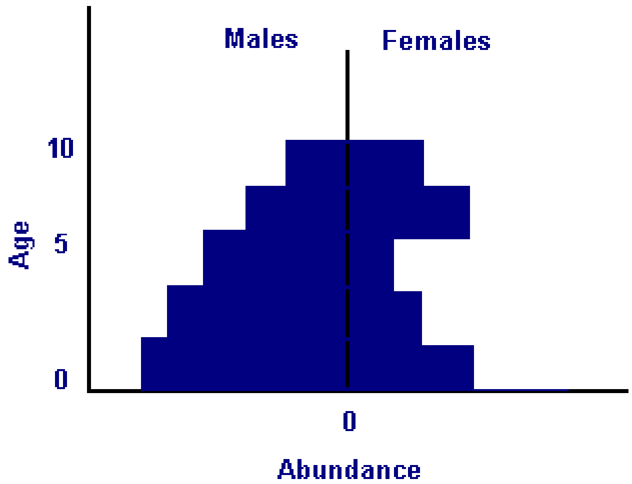


Figure 4



Box 1. Giant Garter Snake Example

The threatened giant garter snake (*Thamnophis gigas*) exists in remnant wetlands in the Sacramento Valley, California. Loss and fragmentation of wetland habitat has extirpated the species from the majority of its historical range. The species now relies heavily on rice fields, irrigation canals, and other managed waterways for habitat. Of the four recovery units, the Sacramento Valley unit is the only unit that is known to support several snake populations that are relatively large and stable. To the south, the Mid-Valley Recovery Unit has only a few small, highly fragmented and isolated populations. Migration between the more stable populations to the north and smaller populations in the Mid-Valley Recovery Unit occurs along canals. The recovery plan (USFWS 1999) indicates these migration corridors are necessary to counter stochastic and genetic threats in the smaller populations. Without this migration, one or more of the snake populations within the Mid-Valley unit would likely be extirpated.

A local water agency has proposed a riprap project along the only canal between one of the larger Sacramento Valley populations and two isolated Mid-Valley populations. The project would destroy or degrade habitat along a five mile stretch of the canal. Although the project is not near any of the snake populations, it would prevent movement of snakes between the populations. Using the BIDE equation, we can show that this could result in extirpation of these two populations in the Mid-Valley unit.

To make this easy, let's assume one of the Mid-Valley unit's populations is currently made up of 100 individuals. The ratio of recruitment through births to recruitment through immigration is 2:3. Again, to make this simple, we'll assume the population adds 100 individuals each year (thus, 40 births, 60 immigrants). This population is a sink, therefore very little emigration is occurring, but many snakes die each year.

Population x is growing by 10 snakes a year:

$$Nt{+}1 = \underset{Nt}{100} + \underset{\text{births}}{40} + \underset{\text{immigration}}{60} - \underset{\text{deaths}}{80} - \underset{\text{emigration}}{10} = \mathbf{110}$$

With the proposed action, the immigration will cease. Within one cycle, the population will be halved:

$$Nt{+}1 = \underset{Nt}{100} + \underset{\text{births}}{40} + \underset{\text{immigration}}{0} - \underset{\text{deaths}}{80} - \underset{\text{emigration}}{10} = \mathbf{50}$$

Compare this to an event that disrupts reproduction within the population:

$$Nt{+}1 = \underset{Nt}{100} + \underset{\text{births}}{0} + \underset{\text{immigration}}{60} - \underset{\text{deaths}}{80} - \underset{\text{emigration}}{10} = \mathbf{70}$$

The population does shrink in this circumstance, but not as severely. If this were a one-time event, the population may have a chance to rebound as opposed to the situation where immigration is permanently cut-off.

Population Growth. Population growth rate is another useful measure of the viability of a population that we can use in our analyses to evaluate the effects of an action. Growth rate is typically reported as either the intrinsic rate of increase (**r**) or the finite rate of increase (**λ**, also called the annual growth rate). If you have adult census information, you can calculate these rates as follows:

$$r = \ln(N_t/N_o)/t \qquad\qquad \lambda = e^r$$

where N_o is the initial population size and N_t is the population size at some time t. For example, a species with an initial population of 320 adults and 95 adults seven years later would have an r of -0.17 and a λ of 0.84. This indicates a declining population (approximately 16% per year), whereas a positive r or a λ over 1.0 would indicate an increasing population and a zero r or λ of 1.0 indicates a stable population. Even if you do not have information on population abundance, but you do know the general trend, you can qualitatively indicate the likely condition of λ or r.

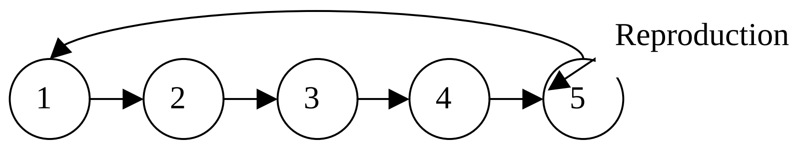
When evaluating population status or responses to perturbation, we also need to consider the variance in population abundance. There is a limit to how much a population can vary in size and still persist. If N fluctuates too violently, the population may "crash" to zero even in populations with positive r. If the variance in population size is greater than 2 times the mean growth rate (mean r), extinction is almost certain.

In addition, a process such as demographic stochasticity, or the variability in population growth rates arising from random differences among individuals in survival and reproduction, is especially important at small population sizes because it doesn't take very many sequential deaths to drive a small population to extinction. Consequently, the probability of extinction depends not only on the relative sizes of births (*b*) and deaths (*d*), but also on the initial population size (N_0). A population's probability of extinction is

$$P(extinction) = \left(\frac{d}{b}\right)^{N_0}$$

If a population had an initial population of 5 individuals, with 0.55 births per individual per year and 0.50 deaths per individual per year (so, more individuals are born than die), its chance of extinction would be $(0.50/0.55)^{50}$ = 0.63 = 63%, a fairly high chance. If another population had an initial population of 50 individuals, with 0.55 births per individual per year and 0.50 deaths per individual per year, its chance of extinction would be $(0.50/0.55)^{50}$ = 0.009 = 0.9%. If a third population had an initial population of 500 individuals, with 0.55 births per individual per year and 0.50 deaths per individual per year, its chance of extinction would be $(0.50/0.55)^{50}$ = 2×10^{-21} = 2×10^{-19}%, an extremely small chance of extinction.

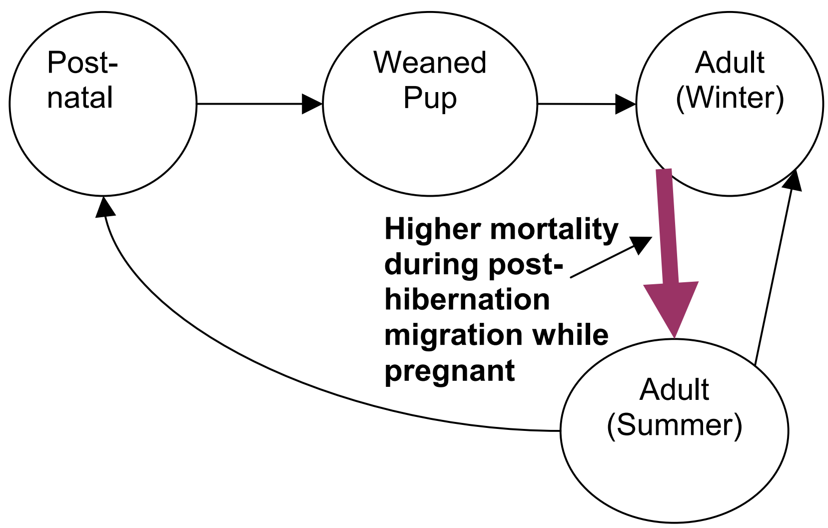
Life Cycle Graphs. Illustrating the life history characteristics of a species is easily accomplished with a life cycle graph. These graphs are useful in our analyses for (1) visualizing the important life cycle stages of a species, (2) displaying the vital statistics associated with life cycle stages, and (3) illustrating or identifying stages or areas of vulnerability. A life cycle graph is a series of nodes connected by arrows indicating movement and fate of individuals through the life history. The nodes represent homogeneous groups of individuals in the populations, classified by age, stage, size, or any other attribute that renders a life-history distinction. The arrows represent movements of individuals between groups or reproduction by one group resulting in additions to the initial group (Hubbell and Werner 1979).



Life cycle models range from very simplistic to extraordinarily complex. The complexity of the life cycle depends on first the specific use of the model, and second, the life history complexity of the subject species (see Hubbell and Werner 1979, Caswell 1982 for examples). Regardless of the complexity, life cycle graphs can be used to identify each critical stage of the life cycle of the species. Our life cycle graphs should identify the assumptions we made, areas of uncertainty or data gaps, and references. Data gaps and uncertainties can be described narratively or graphically (e.g., broken or wavy arrows).

Illustrate any known or suspected life stage vulnerabilities. For some species, certain life stages are especially sensitive to stressors. If known for the subject species or from a surrogate species, it is important to consider these vulnerabilities in our analyses. For example, the mortality rates of adult female Indiana Bats (*Myotis sodalis*) are suspected to be high during their annual spring migration to their maternity roosting areas. This is due to their low fat reserves following winter hibernation, low available food supplies during the migration season, and the increased energetic demands of pregnancy. In a life cycle graph of this species, you could indicate this vulnerable life stage via a different arrow and annotation, as in the example below (Figure 5).

Figure 5.

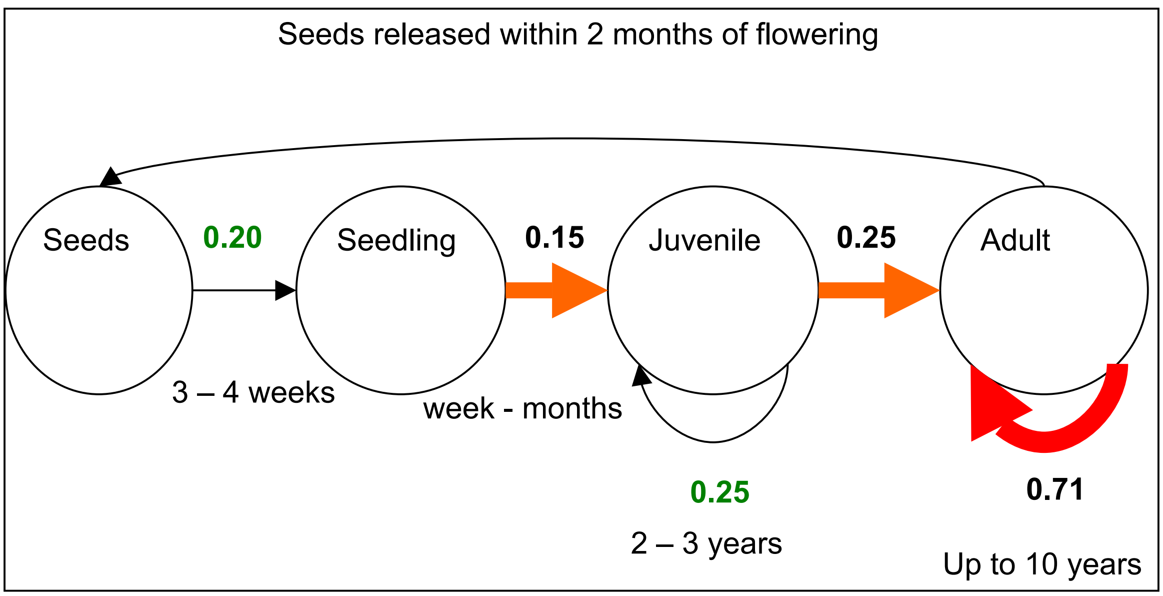


All demographic parameters (e.g., fecundity, survival rates) influence population growth rate, but the extent of influence varies among the parameters and within life stages. These differences are referred to as sensitivities and elasticities. Sensitivity denotes the <u>absolute</u> contribution of each life history parameter to the population's annual or finite growth rate (**λ**). Accordingly, a change in a vital rate with a high sensitivity by a given amount, will change λ more than if you make the same absolute change in any rate with lower sensitivity (Morris and Doak 2002, Caswell 1989). For example, if adult and juvenile survival rates change by 10% and the sensitivity value for adult survival is 0.50 and for juvenile survival the sensitivity value is 0.72, the change in λ would be equal to 0.05 (0.50*0.10) for the change in adult survival and 0.072 (0.72*0.10) for juvenile survival – indicating that λ is more sensitive (changes more) to changes in juvenile survival rates than adult survival rates.

Elasticity denotes the proportional contribution of each life history parameter to λ. As such, the sum of all the elasticity values will equal 1. If juvenile survival has an elasticity value of 0.10 and adult survival has an elasticity value of 0.45, those two rates are responsible for 10 and 45% of the value of λ, respectively. Accordingly, a change in a vital rate with a high elasticity, will change λ more than if you make the same proportional change in any rate with lower elasticity (de Kroon 1986) For more information on matrices and elasticity see Boxes 3 and 4 at the end of this study guide - discussion of most aspects of quantitative population ecology, including life table matrices and matrix math is beyond the scope of this study guide, for further information, the reader is referred to Morris and Doak (2002) and Caswell (1989, 2000). Because elasticities and sensitivities of vital rates greatly influence how an action will ultimately affect a population, it follows that we should be cognizant of these and show them on our life cycle graphs when they are available or inferred based on information from similar species or life histories.

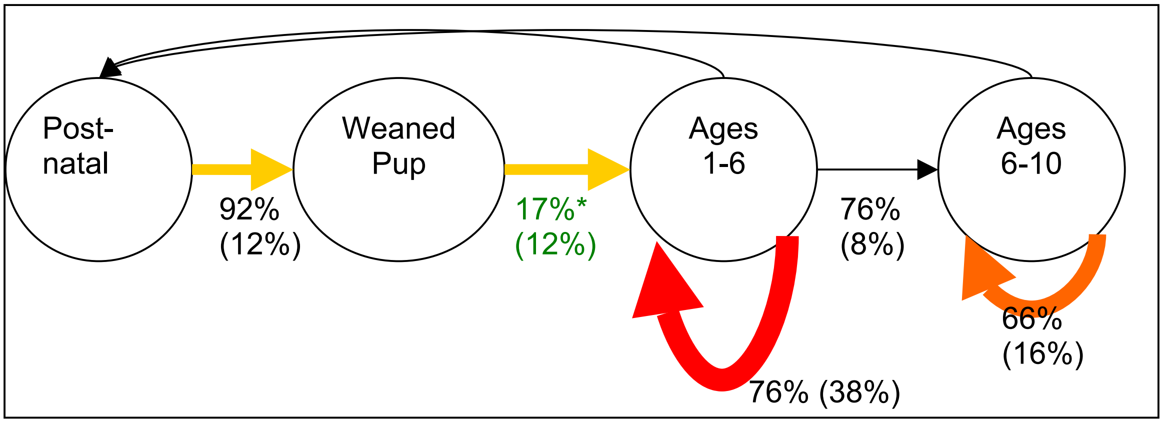
In the Lakeside Daisy (*Hymenoxys herbacea (=acaulis* var. *glabra*)) life cycle depicted below (Figure 6), first and second-most elastic transitions have been denoted by changed colors and thickness of lines (in the examples in this study guide, sensitivities and elasticities were calculated using the PopTools freeware add-in for Microsoft Excel available at: http://www.cse.csiro.au/poptools/). Based on the available information for between and within stage survival rates, and extrapolation of unknown data we can estimate which rates are most likely to affect λ. In this example, changes in the within-stage survival rate of the adult plants have the highest proportional effect on λ. But the difference between highest and second highest isn't very large in this case. The contribution of adult survival to λ is 20% and seedling and juvenile survival are 19% each.

Figure 6.



In the next graph, based on information for the Indiana Bat (Figure 7), elasticity analysis indicates that changes to the within stage survival rates of female adults have the most impact on λ. This finding may not be surprising given the discussion earlier about the highly stressful spring migrations of the females. Further perturbation to those survival rates would have significant effects on the population. Elasticity values for these rates are noted in parentheses below. Note that the weaned pup survival rate of 17% was derived using PopTools to establish a stable stage matrix.

Figure 7.



But it is not always the adult transition rates that have the largest effect on λ. In the following example of the life cycle of Chinook salmon (Figure 8.), absolute changes in the number of smolts that survive their migration to the ocean and the number of alevins that survive to fry stage have the largest impact on λ (highest sensitivity levels are in parentheses, transitions without sensitivity levels had sensitivities less – often much less - than 0.7).

Similarly, in some sturgeon species growth rate is most sensitive to young-of-the-year and juvenile survival and less sensitive to annual adult fecundity and survival (Caswell 2001). Thus, habitat alterations that decrease the survival of young of the year or any class within the juvenile life stage will more strongly influence the affected population's growth rate than if the alteration will only affect fecundity or survival of adults (Gross et al. 2002).

For many listed species, the vital rates are not known. In these instances, it is appropriate and useful to look for data on species with analogous life history strategies such as other populations or taxonomic relatives of the species of concern. Understanding the life cycles of surrogate species can help us make valid inferences about our species. For sea turtles, it is common to use the life history data known for the well-studied loggerhead sea turtle (*Caretta caretta*) when discussing other hard-shelled sea turtles. With Indiana Bats, information derived for other temperate bats is used to fill in vital rate knowledge gaps.

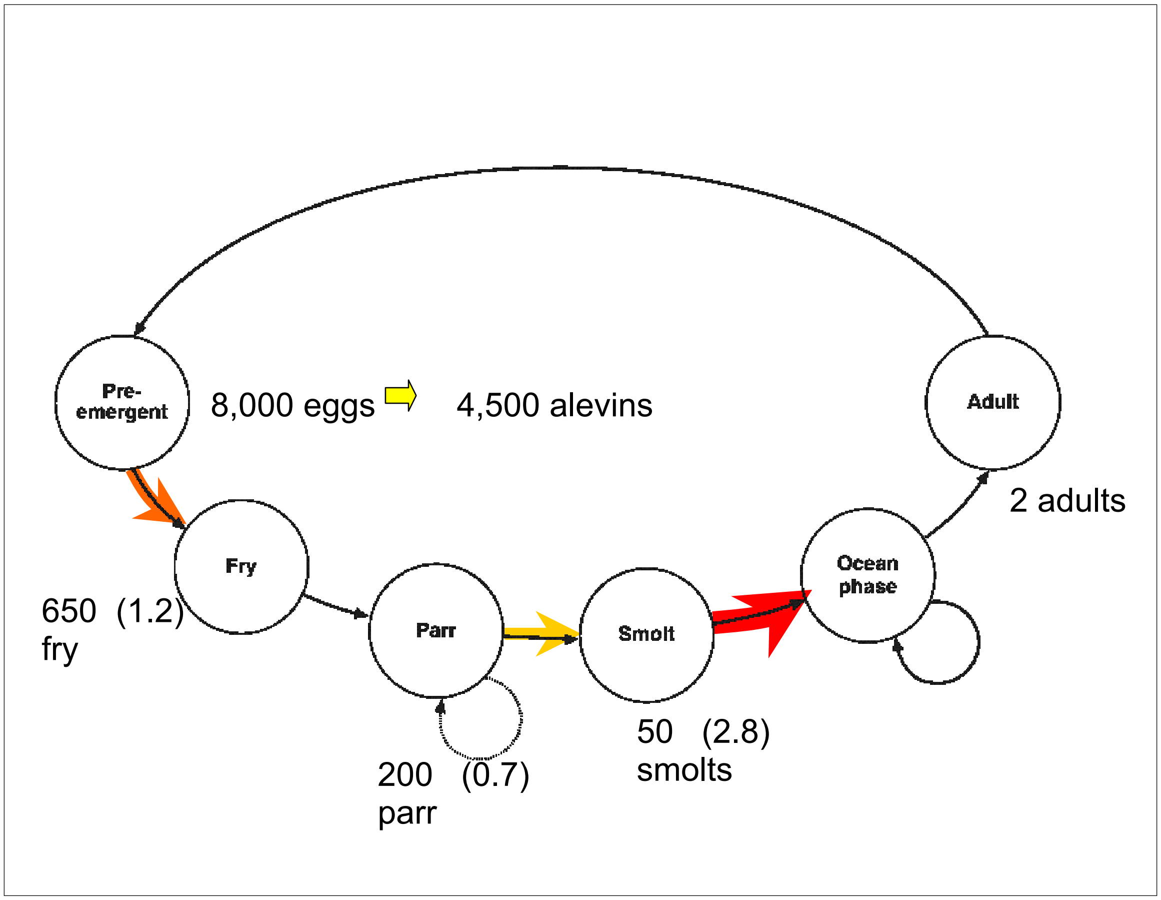
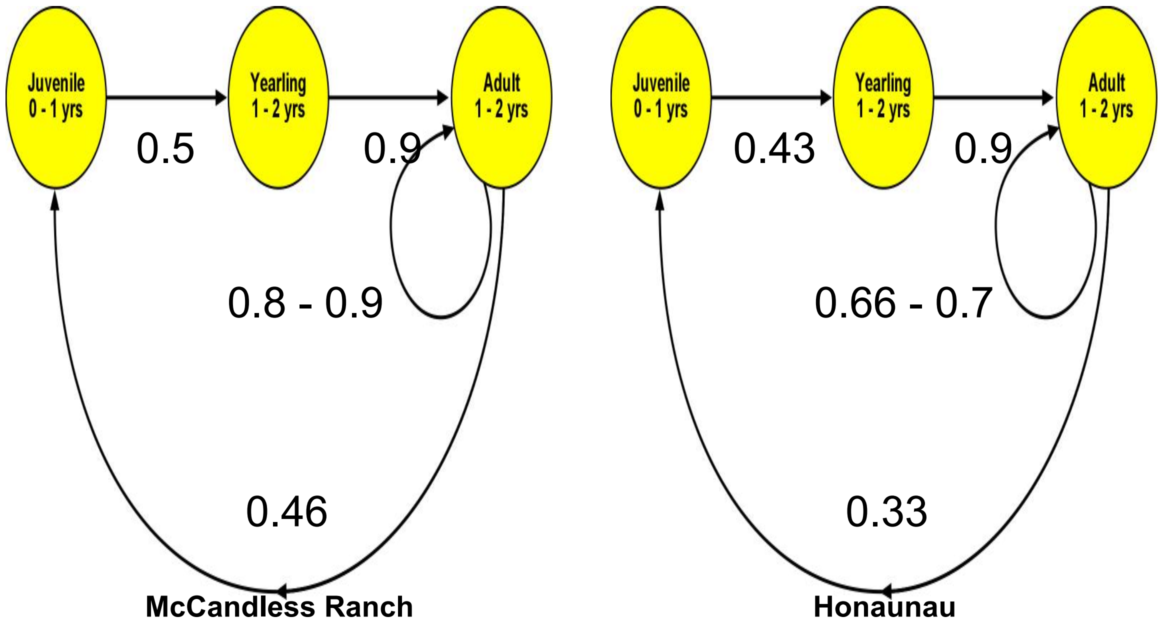


Figure 8.

Sometimes the life cycle, but more often vital rates, has been altered or will be altered in the future. In these situations, it is informative to construct the life cycle as we would expect under normal biological and ecological conditions, as well as under the current or future altered state. Its current or realistic life cycle is needed to fully assess how further changes to one or more vital statistic will alter the life cycle of the species. The “normal conditions” life cycle gives us a picture of how the species evolved to persist.

The below graphs (Figure 9) are side-by-side comparisons of two populations of ‘Alala, the Hawaiian crow (*Corvus hawaiiensis*), one in the wild (McCandless Ranch) and the other in captivity (Honaunau). Based on studies of other corvids, only the McCandless Ranch population had adult survival rates in the ranges found in other healthy corvids. This population more closely approximates the normal conditions of the species (the population was in fact increasing) whereas the captive population was declining due to reduced adult survival, adult fecundity, and juvenile survival. Sensitivity and elasticity analyses indicate that λ in a healthy population was most sensitive and most elastic to changes in the adult survival value. Thus, comparing the life cycle graph and vital rates (known or inferred) for your species or population to those of a healthy population or appropriate surrogate species allows you a way to identify weak spots or areas of particular vulnerability.

Figure 9.



In the example below (Figure 10), an altered life cycle for a salmonid population in a river with a hatchery is shown. The top cycle is the "natural" cycle as discussed earlier in this guide. But note that the reproductive adult stage now has two reproductive vectors, one back to the wild and one into the hatchery population as some wild adults are captured and brought into the hatchery to spawn. These fish are then reared in the hatchery to a certain size, released into the wild, and then return as adults to either spawn in the hatchery or the river. Another life cycle could also be added here to reflect that some of these hatchery adults could stray to another river and contribute to the wild population there. For those adults that return into the hatchery, the cycle is complete and another generation is spawned. For those that spawn in the river, they may spawn with another hatchery fish or with a wild adult. The dashed arrows beneath the wild transition arrows reflect the decreased fitness of these individuals due to selection factors in the hatchery environment.

As a result, the life cycle of the wild population has been altered by the removal of some adults to the hatchery and vital rates may also be affected by the introduction of the hatchery offspring into the wild population, through genetic impacts, intra-specific competition, and disease. The below drawing is one way we can describe our understanding or thinking of how the population operates. Comparing this to a life cycle of a salmonid population with no hatchery influence (such as on the previous page) illustrates the differences and allows us to describe how the population is benefited or degraded by the changed situation.

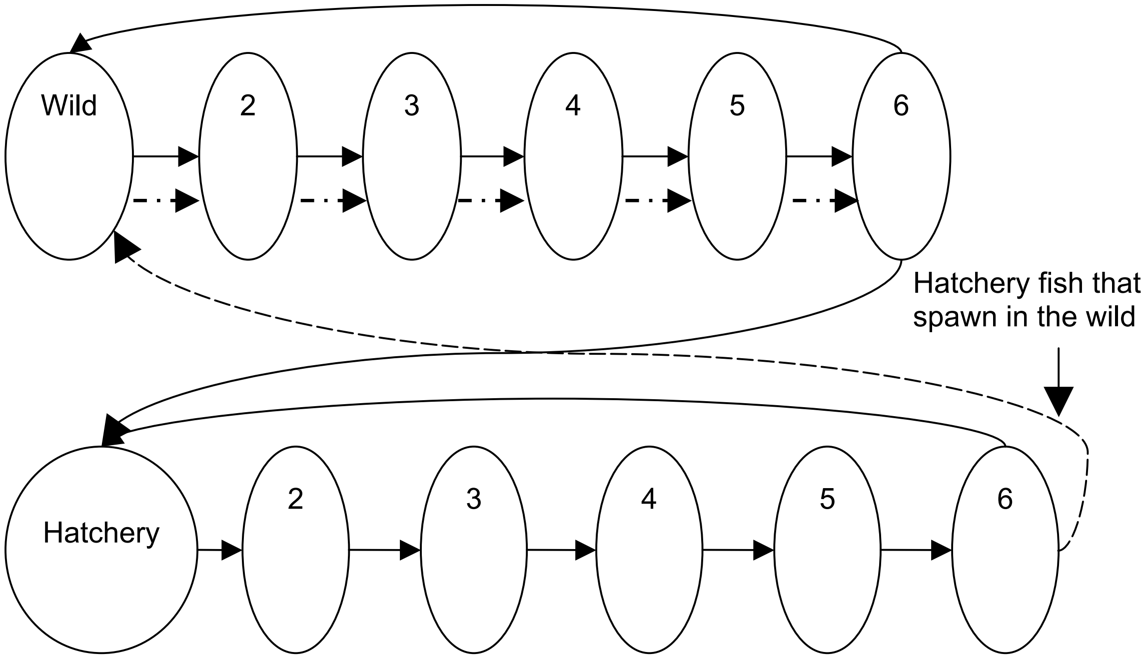


Figure 10.

Habitat Models

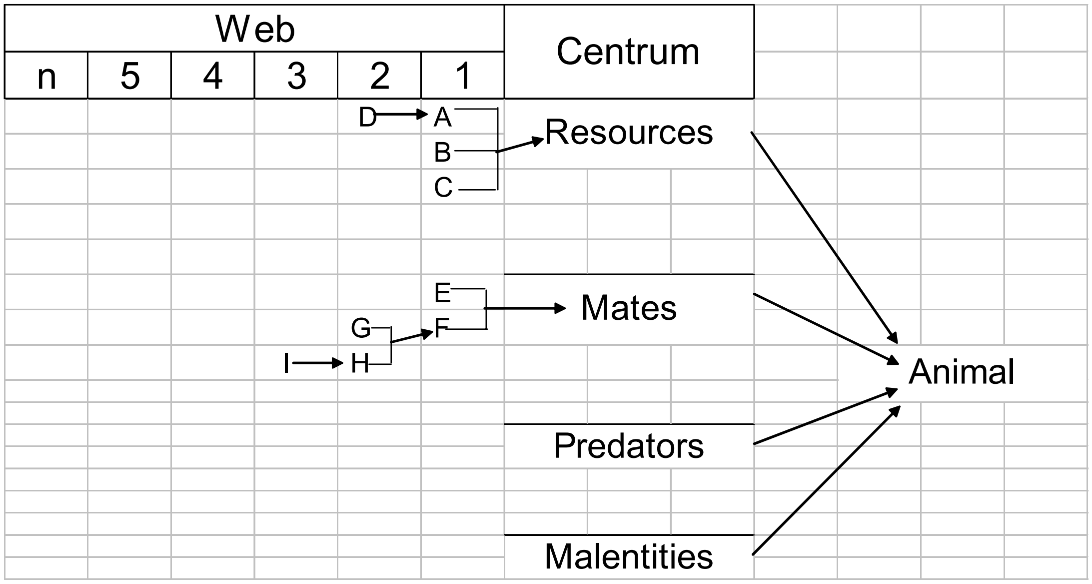
In each of the life cycle graphs above there is a significant amount of information hidden inside each transition, within a stage, or in a fecundity vector. For example, in the fecundity arrow for salmonids are the conditions necessary for each adult pair to successfully produce an estimated 4,500 alevins including such habitat variables as water temperatures, water depths, dissolved oxygen, and substrate permeability in certain preferred or optimal ranges. Conceptual models of the habitat requirements of the species, or of the systems that species inhabit can make this implicit information explicit. There are several types of habitat models, three of which are described below.

Envirograms. Envirograms are a useful way of depicting the ecological relationships that influence the survival and reproductive success of a species (for an excellent introduction to envirograms and an excellent book in general, see Andrewartha and Birch 1984). The environment of an animal is made up of all the things that might influence the animal's chance of survival and reproduction. In an envirogram, the environment is made up of a centrum of directly acting components and a web of indirectly acting components (sometimes called modifiers). Figure 11 is an example outline of an envirogram.

The centrum covers Resources, Mates, Malentities, and Predators (herbivores, carnivores, parasites, and pathogens). These are the components that directly act on the species in that the individual animal's chance of survival or reproduction increases or decreases in response to changes in these components and no other factor or variable comes between a centrum component and the primary animal. For example, if one limpet pushes another off a rock the pushed limpet is now in the sea where it cannot find food, and as a consequence dies. The lack of food is the proximate cause (centrum component) not the pushy limpet.

The web is a system of branching chains made up of living organisms (or their artifacts or residues) or inorganic matter or energy. The web is the ecologies of the organisms or processes that are seen as important in the centrum. For example, wood rats are a centrum component for the spotted owl as they are an important prey item for the owl. Fallen trees, which are important for wood rats, are web components of the owl's envirogram. The ecology of wood rats, including the rat's need for fallen trees and a forage source, would be in the web of the spotted owl, whereas the wood rat itself is in the owl's centrum as a resource.

Figure 11.

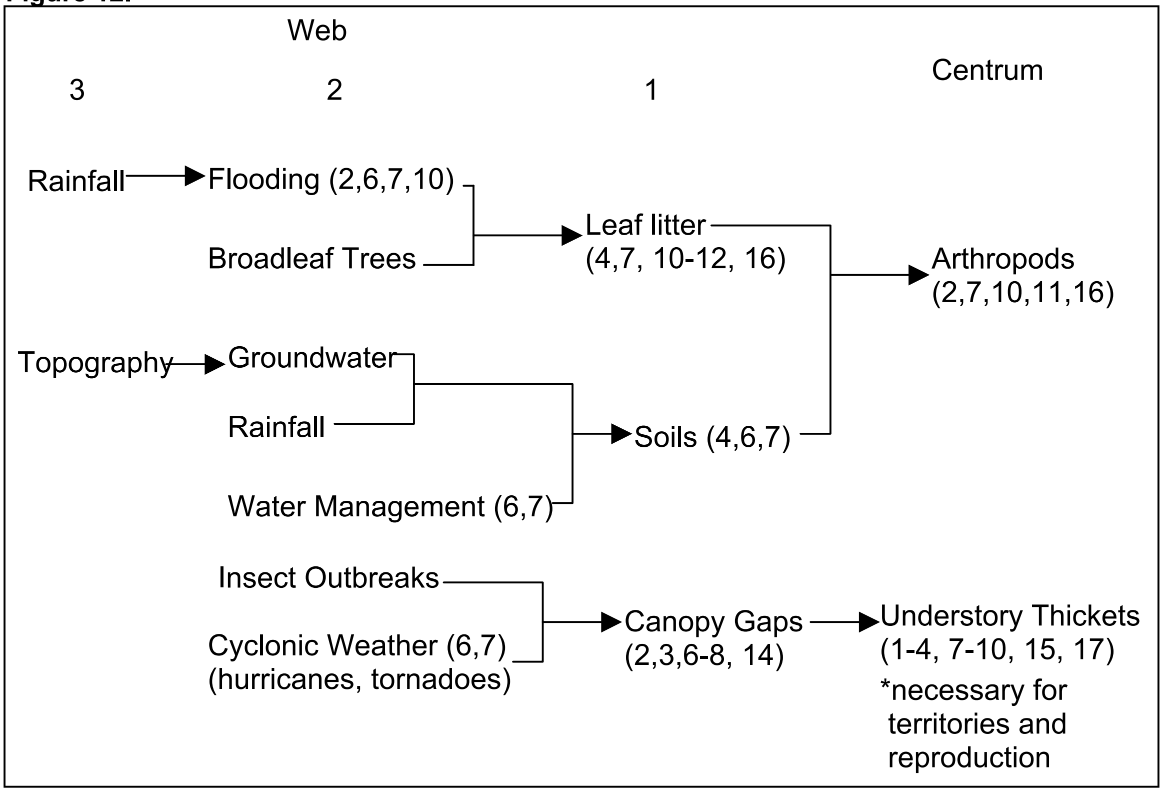


Envirograms are essentially dendrograms concerned with causes. The branches trace pathways between distal causes and the proximate causes of an animal's condition. Each step in the envirogram is a guide or suggestion of information that needs to be verified (or has already been verified) by investigation or supported inference from surrogates. In the partial envirogram for Swainson's warbler below, numbers in parentheses refer to the data source for the pathway (Figure 12).

The envirogram should be a plausible summary of the ecology of the species. For species where we don't know much, the steps are inferred based on our or other's knowledge and provide the guide for future investigation. For species where data has been collected, that is documented, but additional gaps may be identified as well.

To create an envirogram, concentrate on the essential issues – look first for the key components in the centrum and then trace their webs (see Box 2 for further detail on centrum components). It is not necessary to create a whole new centrum and web for each component; put in only what is important or suspected to be so (this goes for centrum components as well). Biologists have a tendency to start at the lowest order of organization, or incorporate the highest level of detail. This is unnecessary for the purposes of the conceptual model we are creating and will add layers of complexity and confusion for those parties trying to follow along. One level of detail you may wish to include, however, are the amounts or levels of the modifiers (where known) that lead to the next link in the chain. For a conceptual model, this is not strictly necessary, but can be helpful information to include particularly for key elements or limiting factors. Creating an envirogram in a program like Microsoft Excel allows you to hyperlink a modifier or connector to a separate spreadsheet where this detailed information is included. This keeps the main image cleaner and yet still provides a source for users/readers to understand the basis of the element or connection.

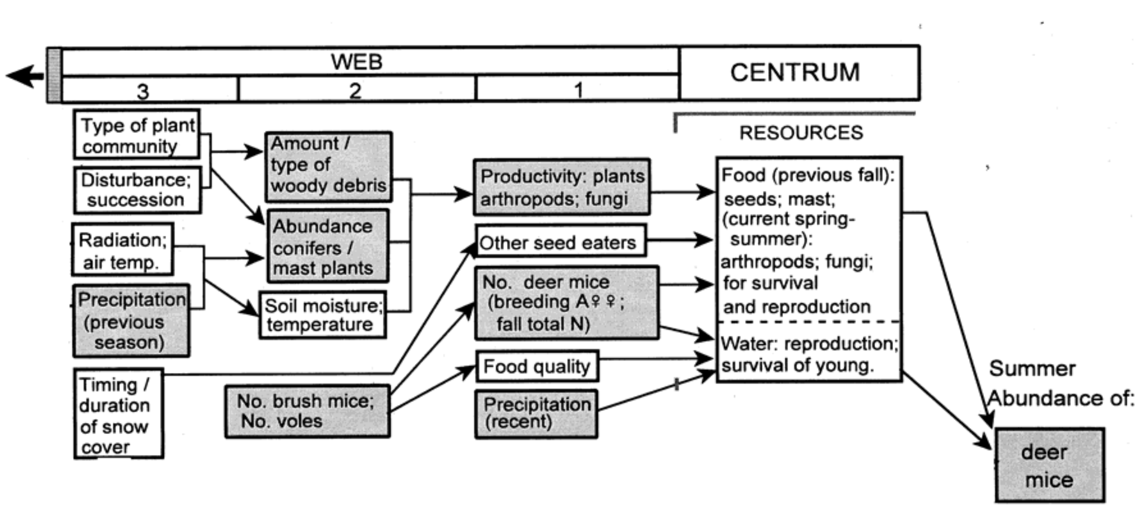
Figure 12.



For species that spend different portions of their lives in different areas, consider creating separate envirograms for each habitat, such as separate envirograms for winter and summer foraging/breeding/etc areas. Consider the different ecologies supporting spiderlings dispersing on gossamer threads versus those supporting mature spiders.

In the partial envirogram for deer mice depicted below (Figure 13), only the summer abundance of the species is included. A separate envirogram covers over-wintering habitat.

Figure 13.



Use concrete nouns as modifiers as much as possible. This avoids the confusion of multiple arrows crossing and criss-crossing across the web and allows the reader to understand the noun's place in the web by which of the centrum components it appears in: a "sheep" may be both food and an agent of dispersal for a tick. Or "heat" may be a resource when the temperature is within the proper range, or a malentity when the "heat" is too high. In either case, the noun would show up as many times as necessary in the envirogram. In the Swainson's warbler example above, the noun "rainfall" appears as a modifier to both soils and leaf litter, which both in turn modify (or support) arthropod prey for the species.

Follow your hunches and use common sense to determine key components in the centrum and web. For example, you may not need to list oxygen in the ecology of a predator in the centrum of a species, since it is likely not limiting. Even food and water may not be limiting or subject to change – use your judgment.

Box 2. Centrum Elements

Resources: Food, water, heat, oxygen, and tokens. Tokens are that which signals to the species that it is time to prepare for the next season, day, next stage in the life cycle, reproductive cycle, cycle of diurnal behavior etc. For example, changes in body chemistry to suit the season, physiological changes in response to changes in temperature, length of day or night, salinity, etc.

Predators: Typically, those that seek out and eat the primary species, and are often specially adapted or equipped to do so. Also includes parasites, viruses, and other similar organisms.

Malentities: These were originally conceived of as "unfortunate accidents" – unintentional harm to the primary species, such as an animal that eats the primary species incidentally or infrequently (Sharks are a malentity for humans, fishing gear may incidentally capture species other than the target species.) Also, generally includes inanimate objects such as an artifact left behind by another animal like deep hoofprints that fill with water and drown insects, or deep ruts in a road, or a road that allows easier access. Anthropogenic impacts are also included where the activity has a direct consequence on the species such as hunters/fishers/collectors or ships and boats that strike whales. Anthropogenic activities where the consequences are indirect (results in changed habitat that in turn affects the primary species) are found in the web, not the centrum.

There is no specific rule on the placement of modifiers in the web, just take care to avoid redundancy. For example, warren construction can modify the predatory fox by affecting the fox's effectiveness at getting to the rabbit or warren construction can be said to modify the rabbit by affecting its evasion capabilities. Pick one – not both.

Also, note that the population of the primary individual or the predecessors of the primary individual may also be in the web (or centrum). For example, the population density may impinge on the availability of food, mates, or cover. The chain below is an example where the preceding individuals of a species have an impact that in turn affects the food resources available to the species today.

Salmon (carcass) → primary productivity → aquatic invertebrates (food resource) → Salmon

To describe the current status of the webs supporting a species, you may need to add additional information to indicate that connections have been broken or compromised. Using the salmon example above, you might indicate that fewer salmon carcasses are available, thereby affecting primary productivity levels, as follows:

Salmon (carcass) ⇢ primary productivity → aquatic invertebrates (food resource) ⇒ Salmon

You can use thickness of lines, type of connector or arrow, footnotes or other notations of your own choosing to denote impacts or changes – just ensure that you also communicate what the notation means. If you have information on the magnitude of the change, note that as well. This is also a place to include the cumulative, or additive, effects of numerous small actions. Years of armoring streambanks or applications of pesticides can be reflected in the envirogram in terms of the types and magnitude of changes they have made to the environment.

Providing a comparison between the “normal” and “perturbed” envirograms makes it easier for users to see what the results of past actions and environmental changes have been and provides a guide towards the future responses of the web to further perturbation. This is particularly useful for analyses of critical habitat and for jeopardy analyses that are primarily based on project impacts on habitat.

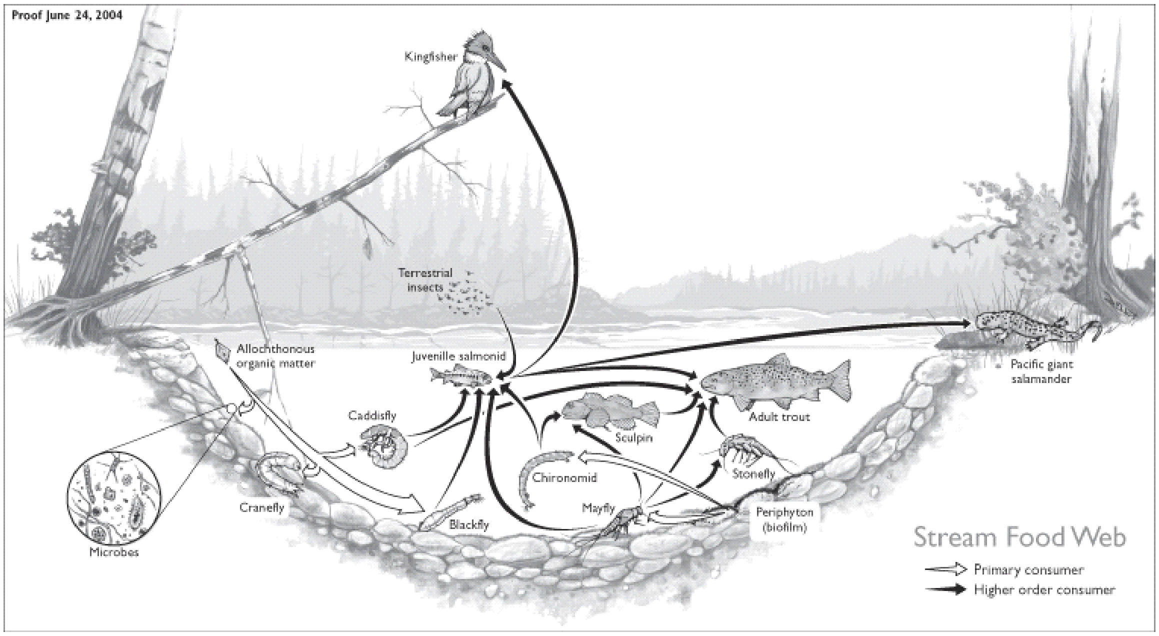
Thus, the envirogram provides the framework or skeleton of the exposure and response analyses, particularly the arguments you are building to establish that an exposure will occur or that the species will have some particular response or range of responses. What you must add to this framework are the relevant details and data to establish that exposure will occur, and the conditions of that exposure are sufficient to result in the response.

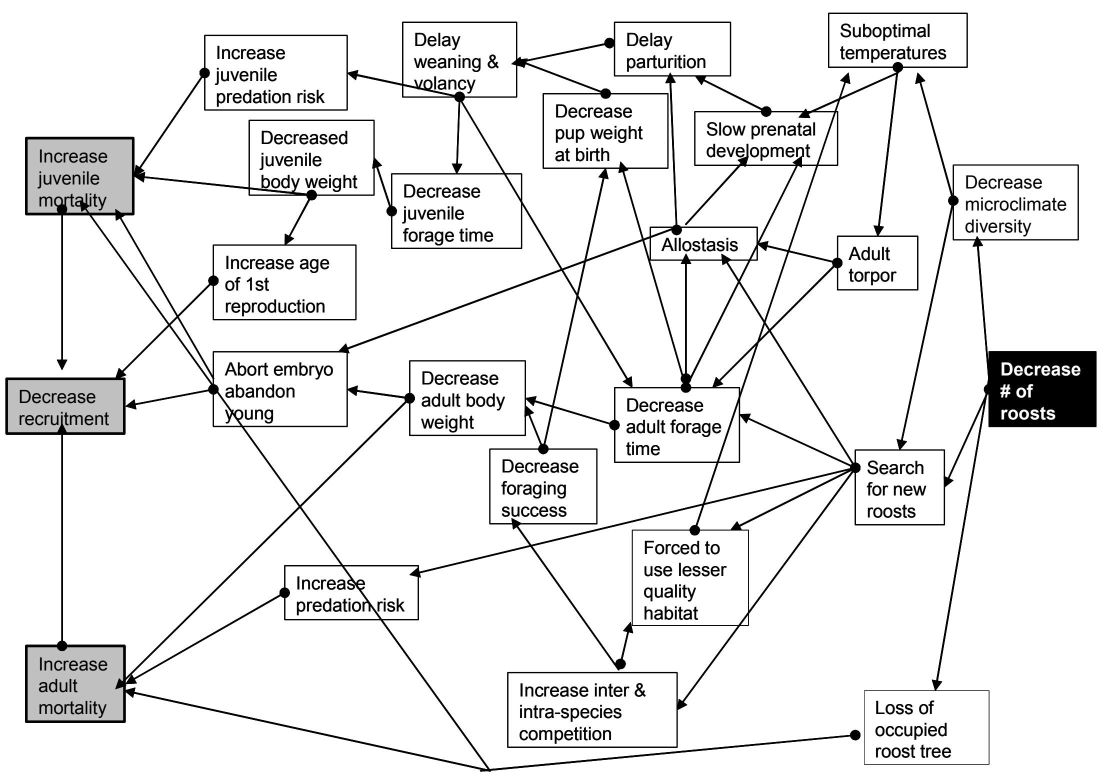
Causal Webs/Food Webs. Other tools that communicate our conceptual model of how a species’ habitat functions and how a species responds to an action include causal webs and food webs. Below are examples of a food web and a causal web.

As with envirograms we can use these models as a way of communicating your understanding of the ecosystem the species depends upon and as a framework for the arguments you build in your analyses. For example, if your listed species was the kingfisher in the food web below, but the action resulted in changes to the substrate structure of the stream (embed gravel with sediment, remove gravels, prevent introduction of gravels from upstream or in-bank areas) then the organisms directly exposed to that stressor would be the primary consumers such as caddisfly or mayfly larvae. If their exposure leads to reductions in their abundance or nutrient level, secondary consumers such as juvenile trout would then have reduced forage supplies. If these reductions are not supplemented by other prey, juvenile trout in the stream would have a reduction in fitness or survival. Similarly, if the loss of juvenile trout prey is not supplemented by other sources, kingfishers would experience reduced survival and reproduction.

Causal webs are also used in this manner. In the example below, the figure draws the connections between a reduction in the number of roosts for a bat and a resulting increase in juvenile and adult mortality and decreased reproduction. By showing all of the intervening steps in the argument, we have outlined the means by which an action impacts individuals and elements of habitat and we have outlined the premises supporting our conclusion.

Food Web and Causal Web





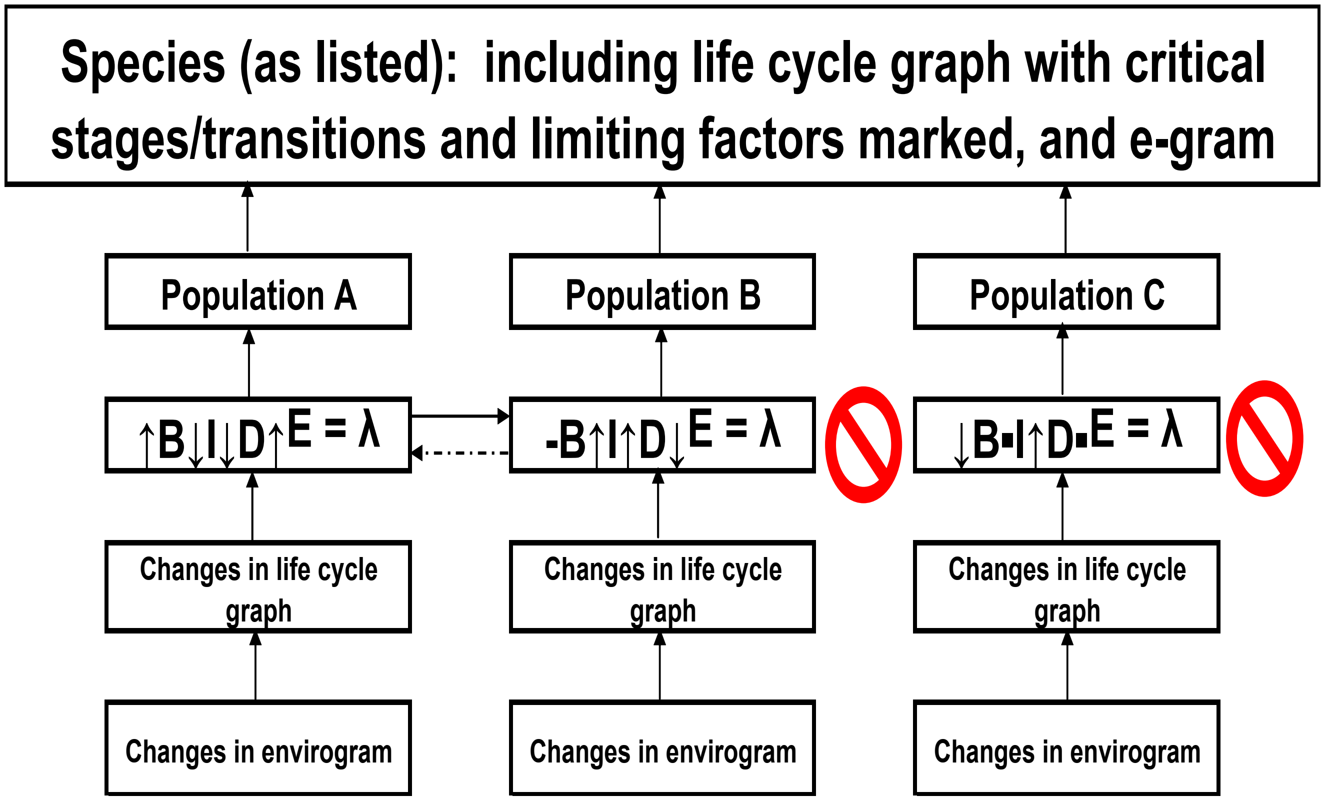
Population Structure

Most species, even "species-as-listed" (Distinct Population Segments, Evolutionarily Significant Units, Recovery Units, etc.), are made up of one or more populations distributed across the landscape. Some species also have various reproductive cohorts within a population (salmonids have different year classes, for example).

Up to this point, we have described several conceptual models that describe individuals, their habitat, and the processes that affect population growth and decline. The combination of these types of models forms part of the structure of our species. Use of a population structure model speaks to the distribution portion of the jeopardy standard ("reductions in numbers, reproduction, or distribution"). Using your model of the population structure of the species, you can argue whether project impacts result in reductions in distribution of the species by increasing the likelihood of extinction of one or more of the populations within that structure.

Population structure includes the number of sub-populations and the connectivity between those populations. The drawing below is a basic conceptual model of a species. The species is comprised of one or more sub-populations that each have their own particular characteristics. Some characteristics may be the same across all populations, and hence for the species, such as life cycle graph and age or sex structure. But there may be variations based on conditions within a sub-population. Those variants make up part of your model of that sub-population. Each population may have its own variation on the BIDE equation. In the example below, you can see that the BIDE factors are modified by some symbol. An up arrow indicates that the rate is high (higher than average, for example), a down arrow indicates that the rate is reduced, a dash indicates the rate is stable, and a square indicates that the rate has a zero value. In the diagram below, immigration into and emigration from Population C has been blocked by some feature or process. There is exchange of individuals between Populations A and B, although Population A provides the bulk of the individuals. Population B has an average birth rate and increased death rate, indicating that the population may be sustained primarily by immigrants from Population A. In other words, Population B can be considered a sink population and Population A can be considered a source population. The assessment can remain qualitative (up and down arrows, for example) as long as we are showing how it is reasonable to make these inferences about the population – the work you have done describing the life cycle or habitat model should help support your inferences.

Based on the conceptual model you construct of the species, you can start to make qualitative assessments of the risks faced by the species before the action occurs. For example, further reductions to the birth rate in Population C, a population that already has an increased death rate and no immigration are likely to quickly result in a lower population abundance and increased risk of extinction (with no hope of rescue from Populations A and B). A similar action in Population B may not increase the risk of extinction for this population if immigration is the primary source of individuals. However, a similar action in Population A likely has adverse consequences for both Populations A and B. As with the other conceptual models, you can use this structure to predict the potential risks posed by an action, and as a framework for the argument you construct to arrive at and defend your conclusion.



Conceptual Models of the Analysis

We can also create a model of the consultation itself by describing our approach to the analysis. This analytical approach guides the use of the ecological conceptual models and also describes how we will gather, analyze, and evaluate the information to answer the questions posed during consultation. For example, the analytical framework at the heart of this class is the conceptual model of the section 7 consultation process. Building off of this framework, you can create an analytical approach for a particular consultation or set/class of consultations.

Analysis Plans. At the initiation of a consultation, or even during the period leading up to an impending consultation, you can create a plan that outlines how you intend to conduct the consultation, what analyses will be conducted (by you or other parties such as action agencies or applicants), which models you may use, which scenarios describing exposure, response, or risk you will evaluate, and how you will ensure that the best available information is used and take into account uncertainty. An example of an analysis plan was included in your binder materials.

Once the analysis plan has been created, you may update or revise the plan after you deconstruct the action or as new information or analyses become available.

The strength of this approach is that you have created a road map of the analyses that others can understand and follow. You can share this road map with the action agency and applicants, solicit their feedback for possible revisions and refine as necessary. Laying out the approach ahead of time creates a transparent process and tends to lead to less confusion on the part of action agencies, applicants, and other stakeholders if they have reviewed and understood the process ahead of time.

Structured decision making. One type of model you may consider using in your consultation is to structure your decision making process by using a variety of decision analysis tools. Consultations are often complex, scientific information may be sparse, there may be a lot of conflicting objectives or disagreement over the best course of action, and uncertainty about the accuracy of our determinations is usually high. Adding some structure to our consultation decisions will enable us to tackle complex projects, improve the transparency of our decisions, improve our subjectivity, and provide a method to treat uncertainties.

Sometimes we don't even realize we're using a structured decision process. For example, a prescribed burn is proposed within habitat of an endangered butterfly the Pawnee montane skipper (*Hesperia leonardus Montana*). The species inhabits dry, open Ponderosa pine woodlands within the South Platte drainage in Colorado. Periodic fire may be necessary to maintain the open nature of the habitat, but there is a concern that the proposed burn will destroy too much habitat all at once. You start listing the pros and cons of the project on a white board. You have started to structure your decision-making process.

Granted, there isn't much structure to brainstorming with a white board. After all, once you've written down everything you can think of, how do you make that final decision whether conducting a controlled burn will ultimately benefit the butterfly? Count up the number of pros versus cons? Gut instinct? Best professional judgment has its place, but more helpful is a process that helps you weigh the advantages and disadvantages of the prescribed burn.

Structured decision making used with a variety of *decision analysis* tools, helps assure a thoroughness and control for biases that are inherent to the human thinking process, particularly during complex and uncertain situations. The process decomposes a problem into its component parts and runs these parts through a series of analysis steps to help determine which choice is most appropriate. By assessing a problem in such an orderly, structured manner, we improve our chances of making rational decisions in situations involving a high degree of complexity and often uncertainty.

That being said, structured decision making does not actually provide the answer. The process will help identify which solutions more closely meet your objectives, but a decision maker must still make the final decision. Of course, because a structured decision making process makes it possible to trace the origins of the decision, if the final decision runs counter to the final outcome of the decision-making process, that inconsistency will be clear in the consultation's administrative record. By now, you should see how the analytical framework at the heart of this class is one such decision structure, but it is by no means the only one!

Structuring decisions:

- gets you closer to your objectives than you could be with intuitive decisions
- forces you to be explicit about measurable objectives
- handles complex problems, especially involving uncertainties
- improves subjective judgments by controlling for biases and decomposing complex questions
- creates more transparent decisions so others – e.g., the public – can understand the reasoning behind decisions
- separates risk evaluation from risk management and makes it explicit when and how each are used
- treats uncertainties explicitly and can link to risk tolerance standards.

Decision analysis tools can be useful not just for the final jeopardy or adverse modification determination, but for steps along the way, such as weighing risk factors or assessing the value of certain evidence for your response analysis. Some ways structured decision making can be used in consultations include:

- contemplating the trade offs of a project's short term risks to the species with anticipated long term gains
- structuring the gathering of unbiased expert opinion when there is little or no evidence
- assisting in clarifying and weighing conflicting evidence
- establishing the relative severity of threats to a species
- assessing the risk of extinction from different actions

The attached study guide on structured decision making provides a more thorough introduction to structured decision making and some of the decision analysis tools available to consultation biologists.

Box 3. Matrix Models, Leslie Matrices

If F_x is the number of offspring born to a mother of age *x* that survive to the next census; P_x is the proportion of *x*-year old individuals that survive to age *x*+1. Then the proportion of individuals in the youngest age class, n_{01}, when the population is censused at time *t*=1 is

$$n_{01} = F_0 n_{00} + F_1 n_{10} + F_2 n_{20} + F_3 n_{30}$$

This is the total of the year's newborns alive at time *t*=1. The individuals in the older age classes at *t*=1 are simply those that have survived through the preceding year, growing older in the process. Therefore

$$n_{11} = P_0 n_{00},\ n_{21} = P_1 n_{10},\ \text{and}\ n_{31} = P_2 n_{20}$$

Summarizing these results in an equation showing the equality of two vectors produces

$$\begin{pmatrix} n_{01} \\ n_{11} \\ n_{21} \\ n_{31} \end{pmatrix} = \begin{pmatrix} F_0 n_{00} + F_1 n_{10} + F_2 n_{20} + F_3 n_{30} \\ P_0 n_{00} \\ P_1 n_{10} \\ P_2 n_{20} \end{pmatrix}$$

This equation implies that each element in the column vector on the left is equal to the corresponding element in the column vector in the right. Next, consider the matrix product

$$\begin{pmatrix} F_0 & F_1 & F_2 & F_3 \\ P_0 & 0 & 0 & 0 \\ 0 & P_1 & 0 & 0 \\ 0 & 0 & P_2 & 0 \end{pmatrix} \cdot \begin{pmatrix} n_{00} \\ n_{10} \\ n_{20} \\ n_{30} \end{pmatrix} = \begin{pmatrix} F_0 n_{00} + F_1 n_{10} + F_2 n_{20} + F_3 n_{30} \\ P_0 n_{00} \\ P_1 n_{10} \\ P_2 n_{20} \end{pmatrix}$$

The right hand side of the equation is identical to the vector in the Equ. XX, which represents the population composition at time *t*=1. The left hand side shows the vector representing the population composition at time *t*=0 *premultiplied* by the projection matrix. This equation can be re-written as

$\mathbf{Mn}_0 = n_1$
$\mathbf{Mn}_1 = n_2$ or generalized as $\mathbf{Mn}_{t-1} = n_t$
$\mathbf{Mn}_2 = n_3$

Where

$$\begin{pmatrix} F_0 & F_1 & F_2 & F_3 \\ P_0 & 0 & 0 & 0 \\ 0 & P_1 & 0 & 0 \\ 0 & 0 & P_2 & 0 \end{pmatrix} = M \qquad \begin{pmatrix} n_{00} \\ n_{10} \\ n_{20} \\ n_{30} \end{pmatrix} = n_o \qquad \begin{pmatrix} n_{01} \\ n_{11} \\ n_{21} \\ n_{31} \end{pmatrix} = n_1$$

Matrix models using this general formula, or using the continuous versions of this formula, form the foundation for sophisticated analyses of populations, including elasticity and sensitivity analyses, population viability analyses, and risk assessments.

Box 4. Elasticity

The sensitivity of a population's finite growth rate (λ) to a change in matrix element a_{ij} is defined as the partial derivative of λ with respect to a_{ij} (Caswell 2000)

$$\frac{\partial \lambda}{\partial a_{ij}} = \frac{v_i w_j}{\langle w, v \rangle}$$

where v_i and w_j refer to the *i*th and *j*th elements of the stage-specific reproductive value (v) and stable age distribution (w) vectors, respectively, and where <**w,v**> is the scalar product of *w* and *v*. The elasticity, e_{ij}, of λ to element a_{ij} is simply the sensitivity rescaled to account for the magnitude of both λ and the matrix element (Caswell 1989)

$$e_{ij} = \frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}}$$

Thus, elasticities predict the proportional change in growth rate given a proportional, infinitesimal change in a matrix element, while all other elements remain constant. The growth rate, λ, is the dominant eigenvalue of the matrix. Because elasticities are partial derivatives, they predict the effect on λ of infinitesimally small and linear changes. Elasticities of matrix elements can be added together to obtain combined effects of multiple changes in vital rates because their proportional nature means that the elasticities of all elements in a matrix sum to one.

Elasticities are usually calculated from a single population matrix constructued from average (or, even, best-guesses) vital rates. As a result, they are only valid for the population contained in the matrix and can become increasingly invalid with populations that deviate from the population reflected in the matrix.

Elasticities can also provide robust predictions of large, proportional changes in vital rates as long as the changes are equal for different vital rates. Unfortunately, all vital rates of a population rarely respond to environmental change in the same proportion or same absolute magnitude. In these cases, the relationship between the changes predicted by elasticities and actual change collapses (Mills *et al*. 1999).

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