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The U.S. Endangered Species Act (ESA) requires that *critical habitat*—areas essential to the persistence or recovery of a species or population—be identified and protected (Goble and Freyfogle 2002). Despite apprehension that requiring critical habitat designation at the time (or within a year) of listing under the ESA would reduce the rate at which species were listed, this does not appear to have happened (Greenwald et al., this volume; Suckling and Taylor 2006). In fact, critical habitat has been designated for only a fraction of listed species (Scott et al. 2006). Reasons for the poor rate of designation include concerns that it provides little additional protection to species (e.g., Hoekstra et al. 2002a, but see Suckling and Taylor 2006) and that sufficient data to determine critical habitat are not available. One problem is lack of a systematic framework for determining critical habitat using various types and amounts of data.

There are two key steps to determining critical habitat. The first is to characterize habitat requirements of a species based on its ecology and life history. Ideally, this is achieved by identifying variables that contribute to presence, density, and demography in different landscapes. The end product is a set of quantitative, functional relationships that predict presence or abundance. When sufficient data are lacking, descriptive habitat preferences based on known occurrences of the species are used to identify habitat requirements and elicit structured opinions from experts.

The second step is to evaluate how different amounts and configurations of habitat affect survival or recovery of the species. In making this determination, different scenarios for the amount and configuration of habitat under protection, and/or characteristics of the population inhabiting that area, are compared to each other and to a criterion, a threshold, or a critical level that embodies an acceptable risk of decline or loss. Again, when sufficient data are lacking, expert opinion can be used, cautiously, to evaluate risks of different scenarios for protecting critical habitat.

The Endangered Species Act mandates designating critical habitat based on the best available scientific data (Ruckelshaus and Darm, this volume). Data availability differs by species, which in turn affects the approach used for determining suitable and critical habitats (Karl et al. 2002; Scott et al. 2002). Models are the primary means of assessing habitat relationships and predicting consequences of habitat change (Wiens 2002). Ideally, sufficient data are needed to effectively determine if the designated habitat would support a viable population. However, often we cannot wait for these data to be collected. As Ruckelshaus and Darm (this volume) point out, logistics of model selection and development for determining critical habitat can be daunting.

In this chapter, we discuss a hierarchical approach to predicting species occurrence and designating critical habitat appropriate for the type and amount of data available to managers.

A Multilevel Framework for Predicting Species Occurrence

Mapping species distributions involves estimation, since it is not feasible to observe presence or abundance of a species across a wide area and because available habitat expands and contracts over time in response to succession and disturbance. Furthermore, individuals might be absent from suitable habitat or occupy suboptimal habitat because of population size, social interactions, historic events, or current pressures. Therefore, mapping species occurrence is an exercise in prediction. Predictive models take many forms, but in the context of mapping species occurrence, three are fundamental: *expert models*, *empirical models*, and *statistical models*.

Expert models rely on knowledge, experiences, and judgment of biologists with expertise in the distribution of a particular species. Although occurrence data are often the basis for defining the predicted occurrence of a species, expert-based maps can possess qualitative and arbitrary elements. They usually define the extent of occurrence of a species or population and are often binary, meaning they show where a species should or should not occur. Range maps published in taxonomic field guides typify this approach.

Empirical models take a quantitative, geographic approach to defining suitable habitat for a species. They infer occurrence from empirical relations describing habitat suitability, usually through use of land cover and other biophysical geospatial data layers entered into a geographic information system (GIS). Empirical models employ two broad approaches. The first, habitat suitability indices (HSIs), describe the suitability of habitat variables, usually subjectively, by experts. They require a priori weighting of individual empirical relations between suitability and habitat characteristics for each GIS layer, such as vegetation type and elevation. GIS layers are combined and analyzed spatially to

define suitable and unsuitable habitat for the species. The second approach uses presence-only information together with GIS layers to create geographic or climatic "envelopes" that transcribe potential habitat (e.g., Elith 2000). In both approaches, various grades of suitability (e.g., high, medium, low) can be modeled, meaning that occurrence becomes a probabilistic prediction, in contrast to expert models. An example is occurrence models developed by the U.S. Gap Analysis Program for a wide range of vertebrate species (Scott et al. 1993).

Statistical models are similar to empirical models in that they infer species occurrence through its association with habitat variables. These models also require use of GIS and geospatial data. Statistical models of occurrence are distinguished from empirical models by the incorporation of numerical or statistical analyses that associate probability of occurrence with habitat resources or other features (e.g., mapped distributions of prey resources). Statistical models take many forms and use different approaches, including multivariate distance and factor analysis methods (Carpenter et al. 1999; Hirzel and Metral 2001), general linear models, general additive models, resource selection functions (Boyce et al. 2002; Manly et al. 2002), and machine learning methods (Elith 2000; Elith and Burgman 2003).

Each modeling approach has advantages and disadvantages. Expert-based models are attractive because they do not require extensive geographic data or a GIS, nor do they require quantitative analysis of species occurrence data. Hence, expert models can be thought of as "data informed" but not "data reliant." However, these models may be subject to biases of expert(s), and the method may have low repeatability.

Empirical models are quantitative and repeatable and hence might be viewed as more scientifically rigorous than expert-based models. However, habitat suitability indices depend on expert judgment, and although more explicit than expert models they still are susceptible to subjectivity and bias. They also may be difficult to perform if expert group consensus is required. Envelopes tend to be biased, overpredicting potential habitat (estimating more habitat than is available) (Burgman and Fox 2003). Empirical and statistical approaches require accessible GIS data relevant to the species, and models may be sensitive to data quality (Edwards et al. 1996; Ferrier et al. 2002).

Statistical models are the least subjective and least biased, relying solely on statistically derived relations between observations of presence/absence or abundance and habitat variables to map a probability surface of occurrence. This process is repeatable and scientifically defendable. These methods, however, can require considerable expertise in statistical analysis. When presence/absence data are lacking, *pseudoabsences* may be generated using a range of algorithms from a random selection of points to more complex methods of inference (Zaniewski et al. 2002). Alternatively, a multivariate technique may be used

that is designed to work specifically with presence-only data (Hirzel and Metral 2001).

A Proposed Multilevel Framework for Designating Critical Habitat

The strengths and weaknesses of each model dictate the approach best suited to a particular situation. For example, if species location and geospatial data are not available, the expert model may be favored. Alternatively, if a higher level of scientific rigor must be achieved, and data are available, empirical or statistical methods may be favored. Generally, one can view the models as representing positions along a continuum of increasing repeatability and rigor, from expert to empirical to statistical, at the cost of increasing analytical complexity and reliance on data. Thus, the degree of scientific rigor is constrained by the burden of data requirements and analytical capability.

We advocate a multilevel framework for achieving the highest-possible levels of scientific rigor (fig. 13.1). Our framework is based on the simple principle that any predictive modeling exercise should begin at the lowest achievable level (i.e., expert model) and build scientific rigor as the data and capabilities of organizations and their personnel allow.

Expert-based approaches provide a foundation for building models of species occurrence grounded in biological expertise and are therefore defendable in

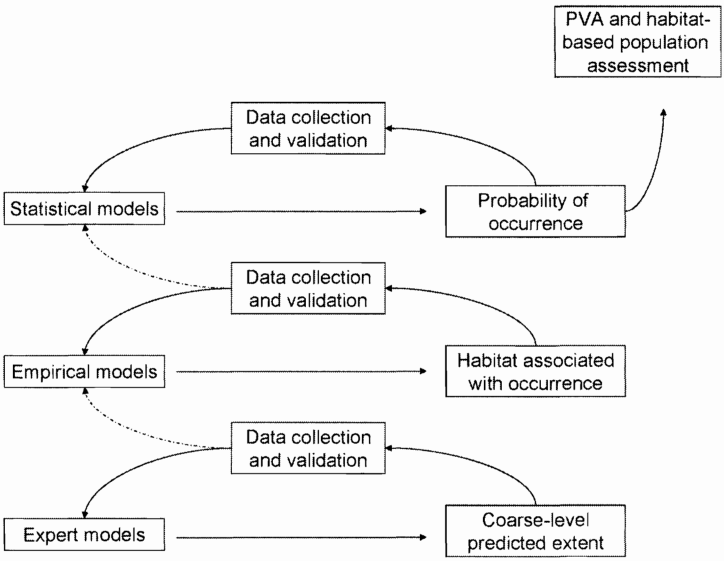

Figure 13.1. Potential framework for predicting species occurrence.

their own right. Over time, experts can identify specific areas of uncertainty where additional data are needed. Thus, the process of making expert maps need not be a static, one-time exercise. Rather, modeling should proceed in an iterative fashion, making use of new data to allow for continual revision, refinement, and independent validation. As with any model, expert models are most accepted when confronted and validated with independent data.

Validating expert models with independently collected data also allows the establishment of databases that accommodate empirically based occurrence models. Like expert models, empirical models can be made transparent and defendable if uncertainties are represented explicitly in functions and on maps (Burgman et al. 2001). Validation data can be used to develop empirical relations between occurrence and habitat suitability. Empirical modeling, like expert modeling, should be an ongoing process; independent data collection and validation are necessary for determining map accuracy and subsequent revisions.

The process of validating empirical models provides additional biological data to construct statistically based models and to represent model uncertainties mathematically and visually (Elith et al. 2002). Observations of species presence/absence used in validation also can be used to build statistical models. Further, the process of creating empirical models facilitates the statistical approach because empirical models provide a guide to which variables are likely to determine the distribution and abundance of the species and the forms of statistical relations they must likely accommodate. For example, the relationship between a habitat variable (e.g., elevation) and a species' occurrence may be quadratic, rather than linear, with a peak in suitability at intermediate values (e.g., a species occupying habitats only at intermediate elevations). Knowledge of the functional relation between a species' habitat and its occurrence is necessary for constructing appropriate models, and, fortunately, this information is often provided from empirical models of species occurrence, such as habitat suitability models.

Statistical models also require validation with independent data before their accuracy can be judged, although this practice seems to be accepted as necessary when using statistical approaches for modeling species occurrence (Boyce et al. 2002). Additional data can be incorporated easily into subsequent runs of the statistical model. As the extent and sample size of data grow, so does model completeness and accuracy (tables 13.1 and 13.2).

Identifying Suitable Habitat Using Logistic Regression

It is common for researchers and resource managers to have location information for a target species, such as those found in breeding bird atlases

TABLE 13.1 Making predictions with available data

Data type	*Uses for data*
Expert information, collateral data, allometric relationships, qualitative trends	Guess *N* (current or target population size), develop conceptual model
Information from cell above, plus single count (census in one time step)	Estimate *N*
Information from two cells above, plus counts over time (census in multiple time steps)	Scalar model (estimate *N*, trend)
Information from all cells above, plus life history information (censuses include data on stage, age, sex)	Structured model (estimate survival, reproduction, *N*, trends)
Any of the above with spatial data	Same models with spatial structure (e.g., habitat-based population viability analysis)

Note: Data are provided in sequence from least to most required.

TABLE 13.2 Deriving statistical models from available data

Data type	*Derived habitat models*
Map(s) and experts	Habitat suitability index
Locations only	Minimum convex polygons, alpha hulls, kernels
Locations and maps of variables	+ climate envelopes, multivariate distance methods, canonical correlation analysis
Locations and random (available) locations and maps	Resource selection function
Presence/absence (used and unused locations)	General linear model (logistic regression), general additive model
Abundance/absence and maps	General linear model (Poisson regression), general additive model
Habitat dynamics	Landscape models (new in recovery context)
All data types	Decision trees, neural networks, genetic algorithms

Note: Data types are presented in increasing order of data need and model complexity.

(e.g., Robbins and Blom 1996), even if data on the quality of occupied habitat and detailed observations on demography are not available. From this, one can quantify variables that might be important to a species, such as elevation, slope, ground cover, and overstory species. Data should be at least taxon specific—meaning they vary by type of species: amphibian versus herbaceous plant versus beetle—but often they are species specific, for instance a known habitat requirement such as salty soils or a den site.

The goal is to use a statistical procedure to distinguish habitat features important for species presence as a means of identifying other sites with similar characteristics that might be suitable for the species. Logistic regression is a statistical procedure that uses data from multiple independent variables (habitat variables in our example) to distinguish between two alternatives (here, suitable versus nonsuitable habitat) (Hosmer and Lemeshow 2000; Scott et al. 2002). Logistic regression can be used with model selection criteria, such as Akaike's Information Criterion, to evaluate a suite of potential models and generate predictions of habitat occupancy by combining inference from multiple models or model averaging (Burnham and Anderson 2002).

Logistic regression requires presence/absence data, but often only observations of species presence are available—usually because more effort is required to identify sites where a species is absent (Reed 1996). Determining the status of cryptic species (for instance, those that are nocturnal, small, or subterranean except when flowering or fruiting) is particularly difficult (e.g., Bibby et al. 2000). Although observed absences are preferred, another solution is to generate pseudoabsences, randomly selected points where presence has not been determined (Klute et al. 2002; van Manen et al. 2002).

The eastern timber wolf is an endangered subspecies of the gray wolf that has been reduced to less than 3 percent of its range outside of Alaska (Mladenoff et al. 1999). A large carnivore with a strong social structure, it lives in packs whose territory can cover 30 to 180 square miles (50–300 square kilometers). Wolves declined throughout their range primarily because of habitat loss from logging, agriculture, and human settlement (Fritts and Carbyn 1995). An extensive database was gathered from radio-collared animals, which provided details of habitat use and ecology. A geographic information system was used to add landscape features of habitat use to the distributional data, providing a platform to infer the potential importance of large-scale habitat features for occupation or avoidance of sites by wolves. Features studied included human population, deer (prey), and road densities. Data were gathered from seventeen to twenty-one wolf packs and compared to fourteen similarly sized, randomly selected sites a minimum distance from known wolf habitat. Logistic regression results showed a number of significant variables such as land ownership class

and human population, with the most important variables being road density and fractal dimension (an index of patch-boundary complexity relative to patch size). This model was then used to identify amount and spatial distribution of suitable wolf habitat in the region. Model validation and improvement is ongoing (D. Mladenoff, pers. comm.).

Using Population Viability as a Criterion for Critical Habitat Determination

The second step in designating critical habitat requires determining whether a particular size and configuration of habitat is sufficient for survival or recovery of the species; such analyses implicitly relate population size and connectivity to measures of viability. The question, How much is enough? as applied to population size and habitat configuration, is perhaps the most difficult problem for the science of conservation biology to answer. First, targets for risk in the form of extinction rates, population size or number of populations, and time horizons must be identified. Then analyses must be conducted to accurately and precisely assess extinction risk from different levels and configurations of habitat. This is the classic "minimum viable population size" problem (Shaffer 1981), which created the field of population viability analysis (Beissinger 2002).

Defining a Viable Population

Viability can be defined as the chance (probability) of species persistence or recovery to a predetermined level. Thus, a viable population is one that has a high probability of long-term persistence or of increasing to a predetermined level. *Population viability analysis* (PVA) is an assessment of risk of reaching some threshold (such as extinction) or projected growth for a population, either under current conditions or those predicted for proposed management. PVAs have ranged from qualitative, verbal processes without models to spatially explicit, stochastic simulation models (Boyce 1992; Burgman et al. 1993), but recently only quantitative, data-based models are considered to be PVAs (Ralls et al. 2002; Reed et al. 2002).

Concerns about appropriate use of population viability analysis have been expressed elsewhere (Taylor 1995; Beissinger and Westphal 1998; Ralls et al. 2002; Reed et al. 2002) and should be reviewed by anyone attempting a PVA. Alternative methods of making conservation decisions, however, are often less able to address uncertainty and may be less transparent about their reliability (Brook et al. 2002; Akçakaya and Sjögren-Gulve 2000). Stochastic (probabilistic) results

of PVA have been evaluated by comparing predicted declines with observed declines of corresponding populations (Brook et al. 2000). Although PVA models can predict short-term dynamics in an unbiased manner, their ability to precisely and accurately forecast the chance (i.e., likelihood) of extinction is much weaker unless the population is growing or declining very rapidly (e.g., Ludwig 1999; Belovsky et. al. 1999; Brook et. al. 2000; Fieberg and Ellner 2000). The likelihood of extinction usually cannot be tested directly with field measurements, but secondary predictions from PVA models can be compared with patterns observed or measured in the field (e.g., McCarthy and Broome 2000; McCarthy et al. 2001).

For application to determining critical habitat for threatened species, viability should be defined in terms of an acceptable probability and time frame, and an agreed definition of persistence (e.g., a population size or rate of change). There are few purely scientific reasons to select particular levels for these parameters; their values are a function of the level of risk aversion or attitude toward risk and uncertainty. They can be based on previous applications or precedence, or on rule-based criteria used to assess threat categories. For example, the International Union for the Conservation of Nature and Natural Resources (IUCN 2003) criteria define a species as "vulnerable" if it has 10 percent probability of extinction within one hundred years. If the goal is species recovery, then a threshold should be defined based on a historical or other socially acceptable level of abundance (box 13.1).

There are also a few technical considerations. For example, probabilities very close to 0 or 1 are difficult to estimate, so "high probability" cannot be defined as 100 percent or a value very close to it. Very long term predictions tend to be uncertain because errors in models are propagated with each time step (usually a year) and the future itself is often full of unanticipated events that are not incorporated into the model. Thus, there is a trade-off between the relevance of long-term predictions and the relative certainty of short-term predictions, so multiple time horizons might be examined with lower levels of risk tolerance for shorter time frames (Ralls et al. 2002). Finally, population dynamics are difficult to predict at low population sizes due to Allee effects, so higher thresholds for persistence are both more precautionary and technically more feasible. For example, viability of a long-lived vertebrate might be defined as the probability that population size will stay above fifty mature individuals for the next fifty or one hundred years.

Determining Viability

Viability of a population or species depends on many factors and interactions among them. These factors can be grouped into four broad classes:

BOX 13.1 Biological and Nonbiological Decisions in Recovery Planning

Setting recovery criteria for endangered species, such as number of viable populations, minimum number of individuals, or minimum distribution of individuals across a region, requires that both biological and nonbiological decisions be incorporated into the process.

Biological Decisions

Defining species, subspecies, populations, and (infrequently) individuals
Defining the management landscape
Identifying threats to population persistence
Identifying sources of relevant data

Nonbiological Decisions

Establishing a time frame for recovery

How far into the future should you evaluate viability? We recommend at least twenty generations *and* one hundred years. Our feeling is that a time frame of at least twenty generations *and* one hundred years would be needed.

Determining the degree of acceptable risk in long-term persistence

How certain should you be that your recovery goal will be effective? The greater the desired certainty, the larger the required population (and therefore more habitat saved) and the more accurate predictive modeling data must be. We recommend at least 90 percent certainty of greater than 90 percent probability of long-term persistence.

Deciding what type of risk to minimize

There are two types of relevant statistical errors (Reed 1996): *Type I error* concludes a species is endangered when it is secure. The cost of being wrong means spending money to recover species not at risk (worse economically). *Type II error* concludes that a species is secure when it is endangered. The cost of being wrong means species could be lost by subsequent actions (worse biologically). One cannot minimize both types of error, so compromise must agree on the acceptable level of risk for both types.

Population size and structure, including the number of individuals; distribution to stages and subpopulations; density of individuals; and trends in population size and structure

Habitat, including quality; amount; and spatial configuration

Demography, including survival; fecundity; dispersal rates, including spatial variation, temporal trends, and fluctuations; breeding system; and sex ratio

Relationships between demographic rates and habitat and between demographic rates and population size

Thus, measures such as population size, population growth rate, or area of habitat capture only a portion of the factors that affect viability. See Ruckelshaus and Darm (this volume) for further discussion.

Using Viability as a Criterion

Viability can be defined as long-term survival of the species, so it is an appropriate end point for designating critical habitat. More important, viability implicitly integrates factors that determine persistence and recovery, namely habitat quality (e.g., the abundance of food resources, levels of contaminants, presence of predators), demography (survival, reproduction, variability, density dependence in survival and reproduction), and spatial characteristics of both habitat and the target species. If a given habitat does not support a viable population, population viability analysis can be used to present alternate management scenarios that create critical habitat, such as changes in the spatial configuration of the habitat, habitat improvement, and increasing connectivity through, for instance, habitat corridors.

Viability can be used as a criterion in designating critical habitat by calculating and comparing viability of the species under different scenarios for the area and spatial configuration of the habitat that would be protected under alternative critical habitat designations (fig. 13.2). Scenarios are ranked in comparison to one another and compared with the viability criteria.

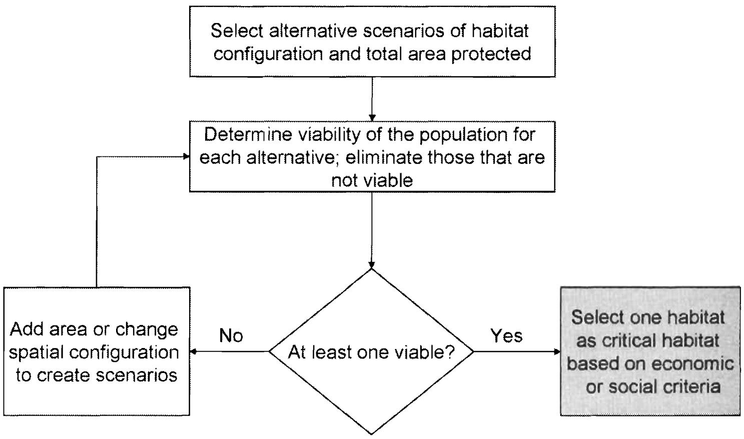

Figure 13.2. Using population viability analysis to compare alternative scenarios for designating critical habitat.

Incorporating Habitat into a Viability Assessment

Incorporating habitat into a viability assessment requires a quantitative description of the habitat (see table 13.2). Habitat models describe suitability of the land as habitat for a particular species. Suitability is usually based on locational information or presence/absence data occurrence or sightings but also can be based on variables such as fecundity.

There are various methods of estimating the habitat model outlined above, each with differing demands for data and technical expertise (table 13.2). The resulting model is one step used to create a map of the species' habitat (fig. 13.3) Habitat models can be validated by estimating them with data from half of the landscape and using them to predict the suitability of locations where the species has been observed in the other half (e.g., Akçakaya and Atwood 1997), or with new field data (e.g., Elith 2000).

A habitat model can be incorporated into viability assessment by basing components of the PVA model, or alternative scenarios, on the amount of and connections between habitats, or on maps of habitat (Akçakaya 2000; fig. 13.3). These components can include spatial structure of the model (number and location of subpopulations), dispersal rates among subpopulations, as well as population-specific model parameters such as population size, carrying capacity, survival rate, and fecundity. Thus, habitat-based population viability analyses have the potential to integrate demographic and habitat models. These models can be used to determine whether a given configuration of habitat is more likely to support a population with a low risk of decline and/or a high probability of recovery than some alternative configuration.

In many landscapes, habitats for most species change over time due to natural processes, such as disturbances and succession, and human activities, such as

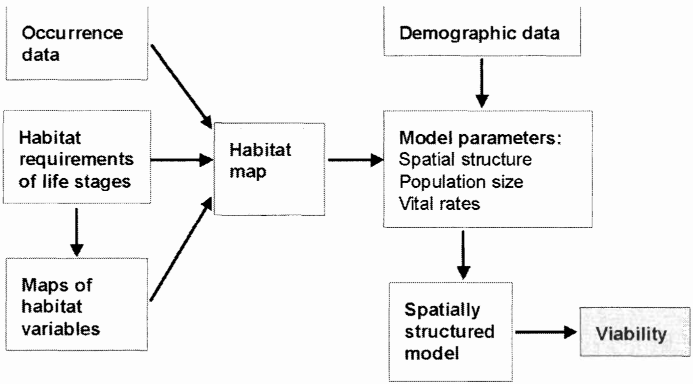

Figure 13.3. A framework for evaluating potential critical habitat using population viability analysis (Akçakaya and Atwood 1997; Elith 2000).

forestry and urban growth. Such changes can be incorporated into viability assessments by linking habitat-based demographic models with landscape models (Akçakaya 2001). Species that live in fragmented landscapes and depend on temporary habitat patches are especially sensitive to both habitat and population dynamics. Viability of such species depends on the balance between the rate of appearance and spatial arrangement of patches and the reproductive capacity of the species. Thus, the only way to assess viability of such species is to consider both habitat dynamics and population dynamics simultaneously.

Caveats to Population Viability Analysis

Population viability analysis is a model, and like all models the assumptions that underlie it should be kept in mind when interpreting results. Consequently, it is important to consider how to translate the results of a population viability analysis into on-the-ground habitat designation (cf. box 13.1). One should not merely take the minimum viable population size and associated habitat; focus on the minimum has long been criticized in the field of conservation biology. Issues of particular importance include problems associated with errors in model structure and data availability, and the stochastic nature of population dynamics. There are many sources of information on—and growing scientific discussion about—accounting for uncertainty in a population viability analysis (e.g., Burgman et al. 1993). None of the methods, however, make quantitative predictions about the minimum population size needed to ensure a suitably low risk of loss. Although not likely significant when comparing differences among reliable, quantitative solutions, and although eliminating risk entirely is not possible, the problem is exacerbated by the difficulty of accurately determining population sizes of some species (Peery et al. 2003).

So, what can be done? Emerging consensus advocates a conservative approach, perhaps taking some value at the high end of a confidence interval. The Marine Mammal Protection Act of 1994 (Act of April 30, 1994) specifies a target population size two-thirds above that of the predicted viable population.

Even if a PVA is practical and a sufficient buffer is placed on viability estimates to reduce uncertainty risk, population size and associated critical habitat might still be insufficient. An ecosystem may require more than a minimum viable population of the target species to create a viable ecosystem. Soulé et al. (2003) introduced the concept of highly interactive species, a new manifestation of keystone species, which play key roles in species interactions and nutrient cycling. Although the concept of a viable ecosystem is not new (e.g., Conner 1988; Loreau et al. 2002; Lomolino, this volume), the idea is not well developed, and sufficient data and methods to determine population sizes needed to maintain ecosystem services and processes are lacking. Soulé et al.

(2003) and Peery et al. (2003) offer examples of how species interactions within a community and the population sizes required to maintain them might be determined.

These arguments support the idea of being generous in initial critical habitat designation and of over- rather than underestimating needed area because of uncertainty, and they describe the asymmetric consequences of being wrong (cf. Reed 1996). An error in one direction could result in species extinction while an error in the other direction could result in loss of resources and opportunities. How large beyond the estimated critical population size this should be is unknown.

Conclusion

Inadequate data to securely determine critical habitat will be a continuing problem. Obviously the more data available, the better will be the proposed designation. A variety of data sources exist, including censuses, surveys, mark-recapture studies, published and gray literature, expert opinion, and occurrence data from Natural Heritage databases. Even data from related species or species with similar habitat requirements can sometimes be used.

In this chapter, we suggested a framework for selecting models to fit available data, but assessment of model effectiveness depends on the question asked. Recovery planning is often about exploring or ranking management options, and in such cases it is more appropriate to instead assess relative risks, which require less precision (Beissinger and Westphal 1998; McCarthy and Broome 2000; McCarthy et al. 2001). Even with insufficient data, a preliminary model is useful for identifying data gaps and research priorities, organizing available information, and focusing discussions. Ultimately, the best evaluation comes from long-term monitoring data and population viability reevaluation to determine if designated critical habitats are supporting viable populations and are expected to do so in the foreseeable future.