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## Chapter 4

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# Theoretical and Statistical Models in Natural Resource Management and Research

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The world is filled with uncertainty. Processes inherently fluctuate. Indeed, the observation system between us and the natural world contains so many sources of uncertainty that even if the processes are certain, the observations are usually uncertain. If we understand theory to be going beyond the data (Peters 1991; Rigler and Peters 1995), then any model—whatever its construction or underlying structure—is a form of ecological theory. Nevertheless, it is possible to classify models broadly as statistical, theoretical, or logical.

*Statistical models* arise in the analysis of data (regression, ANOVA, non-parametric tests, and the like). They are post hoc models (done after the data are collected) and allow the analysis of data. *Theoretical models* posit mechanisms and thus lead to predictions even before data are collected. There are two main reasons for exploring theoretical rather than statistical models: because we wish to understand nature or because the environment is so variable that statistical relationships will not hold. When mechanistic models lead to predictions that disagree with the data, we must rethink the logic of the model or question the data's quality or validity. Statistical relationships

are valuable in situations with low variability—that is, when the model may be expected to work in situations and populations different from the situation of measurement. The way temperature affects growth rate, for instance, may be studied in a laboratory and applied to temperatures in other laboratories and in the field. Statistical models must be treated with caution, however, as soon as the relationship may be influenced by individual behavior. This is particularly true for estimates of natural growth, reproduction, and mortality rates, which are heavily influenced by the activity level and habitat selection of the individuals (Aksnes 1996). To model such phenomena in natural environments, we need theoretical considerations.

*Logical models* are mathematics motivated by the natural world. An example of the distinction between a logical and a theoretical model is the Euler-Lotka model. According to this model, if a population consists of identical individuals for whom fecundity and survival are deterministic variables of age, then the population will grow by a constant rate and reach a stable age distribution. This was first proved via mathematical arguments by Lotka (1925). As a logical statement it is not open to experimental verification, and it holds true within the realms of mathematics. Biologists, however, may investigate whether this model is a good approximation for real populations. For biologists, therefore, the Euler-Lotka model is a theory for population dynamics. Since it does not fit well with observations, an alternative theory for population dynamics has been developed that includes variable environments, individual variability, and stochasticity (Tuljapurkar 1990; Tuljapurkar and Caswell 1997).

Ludwig (1995) has proposed that natural resource management involves at least two paradoxes connected to uncertainties in nature and models:

- Management for sustained yield cannot be optimal.
- Effective management models cannot be realistic.

The source of these paradoxes is “statistical issues and the relationship between models and data” (p. 516). The implication of these paradoxes, particularly the second, is that “statistical considerations generally invalidate any but the simplest aggregated models as management tools” (p. 516). In this chapter we investigate some of the conceptual issues that underlie the paradoxes proposed by Ludwig. Our goal is to lead the reader to a deeper appreciation of the care that must be taken when connecting models and data.

## THEORETICAL MODELS, PREDICTION, AND PARAMETER ESTIMATION

When using theoretical models, we posit mechanisms that connect the independent and dependent ecological variables. Among theoretical mod-

els it is fruitful to treat “why” (ultimate/functional) questions and “how” (proximate/mechanistic) questions separately. Models dealing with ultimate questions address the causes of a phenomenon—which for biology means that these models should be founded in the theory of evolution by natural or artificial selection. Models dealing with proximate questions address how a mechanism operates and resolve the process to a desired level. In estimating mortality, for example, we could construct mechanistic models of the environmental factors that influence mortality risk (visibility, smell, sound, density dependencies). Alternatively, we could construct theoretical models of how Individuals are predicted to act in response to a mortality risk (find the tradeoff between predation risk and feeding rate, for example, as in Werner and Gilliam 1984). By combining these models we can calculate the mortality rate.

Two points, however, are generally unappreciated: a theoretical model is almost guaranteed to be wrong, and there can be many theoretical models of the same phenomenon. For example, the long-standing discussion about “testing the optimality assumption” in behavioral ecology (Gray 1987; Pierce and Ollason 1987; Parker and Maynard-Smith 1990; Brandon and Rausher 1995; Orzack and Sober 1994, 1996) by comparing the predictions of a single theoretical model with data misses the point that there are many optimality models (Hilborn and Mangel 1997; Clark and Mangel 2000). Science progresses by the confrontation of different models with data. The models that are simultaneously the most explanatory (help us understand the data) and predictive (tell us how to find new data by predicting outcomes of new experiments or observations) are the winners and represent our best understanding of the natural world. Theoretical models replace the data of a statistical model by mechanisms, and the best predictions are about new kinds of informative data. We use theoretical models to understand systems and predict their properties.

Data and statistical parameter estimation are components of theoretical models. Ludwig points out, for example, that in order to estimate parameters in a relationship between spawning stock (parents) and recruitment (offspring), we need variation in the spawning stock (see also Myers et al. 1995). Thus it is generally true in fisheries management that the stock cannot be maintained at a single “optimal” level if we need to learn about parameters (Ludwig’s Paradox 1). Similarly, instream flow models, which are used to predict habitat preferences of fish, are a case of a deterministic model that is probably better treated as one in which it is necessary to learn about parameters (Ghanem et al. 1995). Modern statistical methods, particularly those based on likelihood and Bayesian approaches, are well suited for estimating the parameters in theoretical models (Hilborn and Mangel 1997).

Theoretical models are intended to be general—that is the point of focusing on mechanisms. The parameters at a particular site may change, but we assume that the mechanisms do not. Thus theoretical models are intellectually transportable. A theoretical model can fail in the obvious way if it makes predictions that are completely at odds with the data. But a theoretical model may fail in a more insidious way: if a model leads to “exactly what we expected,” without further understanding or prediction, then it has failed. After all, if the results were expected and there are no new predictions, then we understood the scientific question before constructing the model and the model is therefore superfluous. This is why we model: a model of vertical migration that yields an ordinary pattern of diel vertical migration as output has value if the model’s structure explains the forces that are needed to get this result. A good model should explain phenomena at a level previously not understood and should suggest experiments or observations that have not yet been conducted. If we are particularly lucky, then after the model has been developed and analyzed it may be possible to understand the biological situation without recourse to the model (Clark and Mangel 2000, especially chapter 4).

Theoretical models need not be simple. Indeed, the development of high-speed and powerful desktop computing has allowed the construction of individual-based models (Romey 1996; Chapter 12 in this volume) and spatially explicit models (Mason and Brandt 1996) of enormous complexity. They are still theoretical models, however, positing mechanisms to make predictions.

A theoretical model must be able to explain the mechanism and processes of the problem at hand, and its structure and detail must have a biological (or physical) interpretation and be measurable (at least in principle). Formulating a theoretical model—specifying the mechanism, constraints, and parameters—is an exercise by itself, and a fit to data is not the only criterion by which the model is evaluated. Although we can investigate the internal consistency and predictions from a theoretical model, a theory can be tested for relevance to natural phenomena only through normal scientific progression—that is, by formulating alternative hypotheses, outlining critical experiments (or searching for field observations to evaluate hypotheses), and then letting the data adjudicate the hypotheses (Platt 1964; Mangel and Clark 1988; Hilborn and Mangel 1997). We should not evaluate theoretical models solely on how well they fit the data: there are other grounds as well, such as elegance, internal logic, and explanatory power. If a consistent theory does not compare favorably with all the data, we should reconsider the data and the way they were acquired before rejecting the theory. This is especially relevant when no alternative theory is available or when the alternative theory is not consistent or simple or

supported by other sources. Natural resource ecology and management is a complex matter. No matter how expanded our model, we cannot expect more than partial overlap between the model and field or laboratory data. This point is related to Ludwig's second paradox: when we need to estimate parameters, smaller (and simpler) management models often perform better than more complicated ones.

In a variant of the approach used here, Loehle (1983) divided the models along a continuum between the "application" model and the "calculation" model. An application model uses laws and theories to make predictions about a phenomenon; a calculation model can be as simple as a statistical regression without any notion of mechanism. Because they are more general and apply to a wider range of situations, application models are superior to calculation models.

In general, theoretical models provide a deeper level of understanding than statistical models. This is not always reflected in the quality of fit to data, however. If we are most interested in a close fit to the data, we should choose a statistical model because it allows us to modify all parts of the model to achieve this goal. As we start to adjust theoretical models, however, they lose their explanatory power and gradually become statistical models. The implication is that science should aim for theoretical models (Giske et al. 1992; Giske 1998)—while always making explicit the processes and parameters that weaken the level of understanding expressed through the model. This is an important part of the modeling process: to clarify what is known and what needs further elaboration. Since theoretical models should be formulated in biologically meaningful terms, they indicate what needs to be measured in order to settle parameter values. Once these values are defined and measured, the modeler is no longer free to change them.

### STATISTICAL MODELS AND EFFECTS

Statistical models are typically without a mechanism, although they posit relationships between variables. Imagine a set of data  $\{X(i), Y(i); i = 1, \dots, n\}$ , where  $X(i)$  are the presumed independent variables and  $Y(i)$  are the presumed dependent variables. The statistical model answers the question "Does  $Y$  change as  $X$  changes?" (or some variant of this); this is what most ecologists do. Even with statistical models, this question can be answered in a number of different ways. That is, there are many statistical models for a phenomenon. In null hypothesis testing, for example, we begin by hypothesizing that there is no relationship between  $X$  and  $Y$  (the null hypothesis) and then use the data to determine the probability of observing data given the assumption of no relationship. If this probability is small enough, we say



the hypothesis of no relationship has been “rejected” (see also Gotelli and Graves 1996). Note that this does not actually deliver the goods. What we would ideally like to know is the probability that a hypothesis (say, that  $X$  increases as  $Y$  increases) is true given the data. What we get is the probability of observing the data given that the null hypothesis (in this case of no relationship) is true (Cohen 1994; Royall 1997).

Nonparametric statistical methods deal with the data only. Parametric statistical methods posit a statistical relationship such as

$$Y(i) = \beta_0 + \beta_1 X(i) + Z(i) \quad [4.1]$$

where  $\beta_0$  and  $\beta_1$  are constants and  $Z(i)$  represents the uncertainty in the system. Alternatively, we might posit a log-linear relationship in which the logarithms of the variables are linearly related. Equation (4.1) is generalized in a relatively straightforward manner when there is more than one kind of independent variable. Suppose that  $X_1(i)$  and  $X_2(i)$  are two different independent variables. The generalization is

$$Y(i) = \beta_0 + \beta_1 X_1(i) + \beta_2 X_2(i) + Z(i) \quad [4.2]$$

This is called a model without interactions, because no combinations of  $X_1$  and  $X_2$  appear. There is only one model without interactions but an infinite number of models with interactions because the interaction can be characterized by any function of  $X_1$  and  $X_2$ . Hence researchers typically concentrate on models without interactions (see also Hilborn and Mangel 1997). Bradford et al. (1997), for example, used a combination of statistical models to develop predictions about the relationship between abundance of coho salmon (*Oncorhynchus kisutch*) smolts and stream characteristics such as length, gradient, valley slope, latitude, and minimum and maximum flows.

Statistical models are driven by data. For this reason they are specific to the location and the system studied. Their details are not intellectually transportable, although the general approach may be. Indeed, Roughgarden et al. (1994) argue that we should view ecology more as an earth science (in which every setting is unique and controlled as much by geological transport processes as by biological species interactions) than as a molecular biological science (in which every experiment is reproducible anywhere). But care must be taken. Kozel and Hubert (1989), for example, identified the physical and biological factors that appeared to control the density of brook trout (*Salvelinus fontinalis*) in drainages in Wyoming. They found a suite of 18 variables that were significantly ( $p < 0.05$ ) correlated with brook trout standing stock and developed individual regression equations for each of them. They also discovered 25 significant correlations between the variables, but they provided little theoretical underpinning for

the statistical relationships. Fine so far; this is a statistical model. Now consider their last sentence: "The relationships presented by us can be used as standards for comparison when assessing abundance of brook trout in streams altered by human activity or when determining mitigation objectives for such streams." By advocating not the approach but the relationships, they changed a statistical model into a theoretical model with little evidence that this change is valid.

### AVOIDING THE PITFALLS

There are a number of ways to avoid getting trapped by Ludwig's paradoxes, which remind us of the care that must be taken when connecting models and data.

#### Avoid Too Many Uncertain Parameters

Ludwig (1995) points out the dangers of overfitting data and notes: "Having the correct model is not enough: the associated parameters must be well determined" (p. 521). Picking the right size for a model is a developing art (Hilborn and Mangel 1997). This applies to statistical models (Hakanson 1995) and to theoretical models for which parameters must be estimated. If the physical or biological parameters are not known or are measured with great uncertainty, it is even more important to keep the number of parameters low. With well-defined and independently measured parameters, this is less critical.

There is always a tradeoff between simplicity and the level of mechanistic description. This is what leads to Ludwig's second paradox. In general, simple models are attractive because of their tractability and transparency and should not be abandoned too quickly due to dissimilarities with empirical studies (although our unease with the model may increase). A mechanistic model of the functional response in fish was developed by Aksnes and Utne (1997), for example, and the derivation clarifies the importance of the optical properties of water in understanding the distribution and dynamics of fish and zooplankton. In this case, the level of elaboration was justified by the influence of the model's details on the predictions—conforming to the rule that we should keep models simple unless there are good reasons to do otherwise.

This argument can also be applied in the discussion of whether a model should be formalized computationally or analytically. With analytical models, we are more likely to be able to control and verify the results directly from the derivation, whereas numerical models may carry flaws in the computer realization that are not easily detected. Analytical models are

often more elegant and parsimonious in the sense that they may be resolvable without aid of computers (at least in principle). This is also the limitation of the analytical approach, however, because the simplifications are made at the expense of realism. Numerical models allow much more biological detail and realism and permit investigations of many questions that cannot be asked analytically. General principles can be drawn from numerical modeling through the performance of "computer experiments" and sensitivity analyses (Mangel and Clark 1988; Hilborn and Mangel 1997; Clark and Mangel 2000).

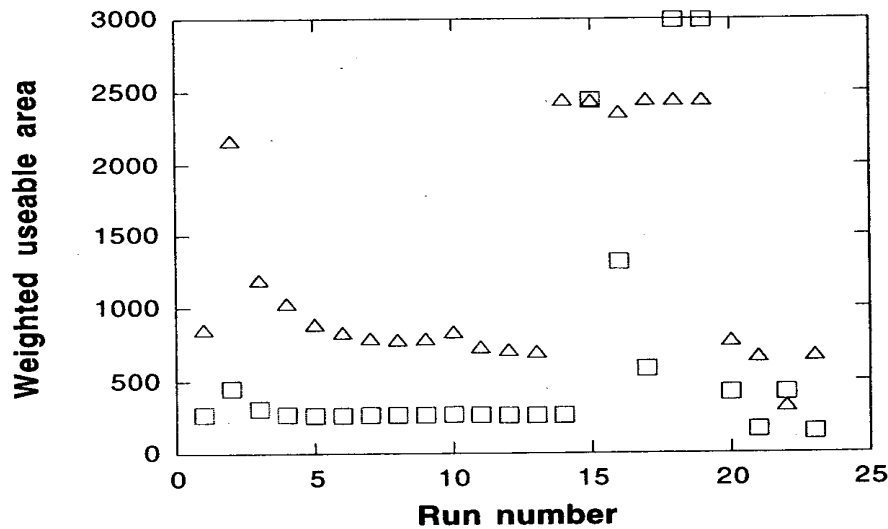
### Always Try to Compare Multiple Models with Data

Chamberlin (1897) argued that we should always have multiple working hypotheses. As we have seen, theoretical models almost immediately lead to multiple models as different mechanistic formulations are envisioned. Statistical models can do the same, if we posit different relationships, but without a mechanism. Myers et al. (1995), for example, confronted four different models of recruitment and two different models of uncertainty with more than 250 sets of stock-recruitment data. This method allowed them to determine the most appropriate description of the functional relationship between recruits and spawners and the most appropriate conceptualization of the variability in recruitment.

Gan and McMahon (1990) showed that the Physical Habitat Simulation System (PHABSIM) used for instream flow analysis actually consists of a large number of different logical and statistical models (based on which subprogram is used), assumptions about how velocity, depth, and substrate are related to weighted usable area (WUA), type of velocity profile, type of velocity equation, and bed material. Using a single set of hydraulic data and preference curves, they investigated 23 combinations of variables and discovered (Figure 4.1) a nearly tenfold range in predictions of WUA for fry and juvenile brown trout (*Salmo trutta*). They noted (p. 233) that the "results are shown to vary greatly according to the particular combination of options selected, so unless calculations are founded on biologically realistic assumptions, the potential within PHABSIM for the 'fudging' of results is considerable." Thus it is essential to have agreement on biological assumptions before computations are done (Mangel et al. 1996). It is even more important, however, to evaluate the models by confrontation with data (Hilborn and Mangel 1997).

The same is possible for statistical models. Rahel et al. (1996), for example, used a statistical model to predict habitat loss and population fragmentation in the North Platte River drainage by constructing statistical relationships between geographic area lost based on air temperature, stream





**Figure 4.1.** Gan and McMahon (1990) investigated different predictions of weighted useable area (WUA), computed from PHABSIM, for brown trout (*Salmo trutta*) fry (squares) and juveniles (triangles). Different assumptions in the underlying logical model are used in different runs of the program. Note that the WUA for fry may differ by a factor of 10 and for juveniles by a factor of nearly 8.

distance lost based on air temperature, and stream distance lost based on water temperature. They noted that the three approaches gave different predictions of the amount of habitat loss due to climate warming and then used theoretical methods to sort out some of the variation in the predictions of the statistical model. Lek et al. (1996) conducted a similar study, using statistical models involving up to eight variables, to relate environmental parameters and trout abundance.

## Always Be Thinking of Alternative Models

Logical models are tested with mathematics. Theoretical models are tested by experimentation and observation. The models we use in management and ecology are often complex. For these, it is better to test each of the major assumptions rather than try to test the predictions of the models. This has to do with the incomplete overlap between model and environment and the hopeless task of measuring the relevant environmental complexity in an instant. We should always recognize that the model may miss a key feature of the natural system—even one that drives the full behavior of the system.

An example of this research strategy is the study of eutrophication in the North Sea (Aksnes et al. 1995). Starting from the Holling equation describing the feeding rate in animals, Aksnes and Egge (1991) developed a mech-

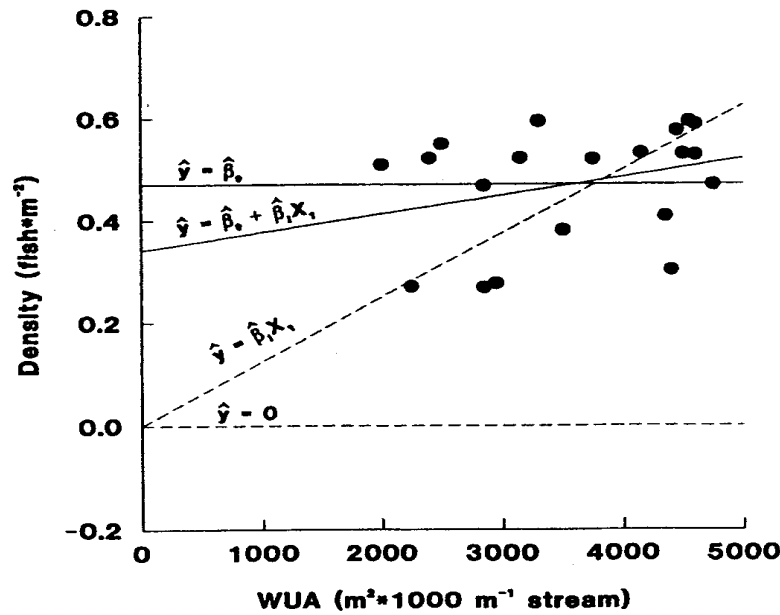
anistic model for nutrient uptake in phytoplankton. Parameters were estimated for two groups of algae (diatoms and flagellates) such that the parameters (which have precise biological interpretations) were fixed from measurements (Aksnes et al. 1995). Simultaneously, many series of enclosure experiments were conducted with a wide range of nutrients (Egge and Aksnes 1992; Egge et al. 1994), and the time series of phytoplankton abundance was compared with predictions from the model. No tuning of the parameters was allowed, since the intention was to develop a general tool for the study of eutrophication. The model has now been incorporated into a three-dimensional physical model of the North Sea and applied to investigate issues related to eutrophication and management (Aksnes et al. 1995; Baliño 1996).

Similarly, from the predictions of a model of an experiment studying migration and allocation patterns in *Daphnia magna*, Fiksen (1997) suggested that the daphnids maximized rate of increase ( $r$ ) rather than net reproductive rate ( $R_0$ ). In the model (and experiment), growth was a function of temperature, with 98 percent of the variance explained by temperature. Mortality risk from fish was an encounter-based model with measurable parameters such as image area, ambient light, and predator density. The model did not match the data very well without the assumption of decreasing mortality with increasing size, which would occur if there were invertebrate predators present or if the daphnids live according to this potential threat. Thus with well-defined environmental forcing and physiological response, the model and the data could be used to investigate assumptions about the shape of the predation risk and the optimality criterion. By further mechanistic modeling and corresponding fixation of parameters, the number of assumptions was reduced and the model improved for applications.

In summary, then, instead of talking about models being false or true, we should talk of good or bad models—evaluated by their explanatory power and ability to predict observations. In practice, models that are considered good (often the simplest models) are not rejected even if observations do not confirm their validity (Lotka-Volterra models of population dynamics, for example). Some models are retained even though there are hardly any observations that fit the predictions (Fagerstrøm 1987). Finally, models and theories tend to be used as long as there is no better theory to apply (Lakatos 1978; Hilborn and Mangel 1997). For this reason we should always be thinking about alternative models.

## Don't Go Where the Data Aren't

Both theoretical and statistical models may enter intellectual quicksand when applied to situations where there are no data. Consider, for example,



**Figure 4.2.** Forcing a regression equation to show the origin can be very dangerous if there are no data in that region. Doing so essentially converts a statistical model to a logical model, perhaps unintentionally. (Reproduced from Cade and Terrell 1997.)

a stock-recruitment relationship between parents in year  $t$  ( $S_t$ ) and offspring in year  $t + 1$  ( $R_{t+1}$ ):

$$R_{t+1} = aS_t e^{-f(S_t)} \quad [4.3]$$

The parameter  $a$  represents maximum per capita reproduction when population size is small;  $f(S_t)$  captures the density dependence of reproduction. The form of density dependence has to be estimated. The trouble is that the parameter characterizing behavior at a small population size is usually influenced by observations far from the origin (and vice versa: Levins 1966). As a solution, Myers et al. (1997) propose that we should use only the six observations with the smallest spawner biomass. When a model has a strong theoretical basis, we should not feel obliged by the data to apply a simpler relationship. Rather, we should use the theory to suggest investigations that will find data in an area that is relevant for discrimination among the competing models.

Similar problems arise with statistical models. Cade and Terrell (1997), for example, point out that by forcing a regression through the origin by setting  $\beta_0 = 0$  in Equation (4.1) or (4.2), we may generate an apparent relationship between fish density and weighted usable area even though there are no data to support this (Figure 4.2) (see Bourgeois et al. 1996; for examples in evolutionary ecology see Charnov 1993 or Mangel 1996).

## Don't Confuse Statistical and Theoretical Models

The error of mixing statistical and theoretical models is called “the error of pseudo-explanation” in Loehle (1987); Dunham and Vinyard (1997) make a similar point. It is possible to conduct an excellent and elegant study using a statistical model but then to conclude wrongly that you have constructed a theoretical model. As we have seen, forcing the regression through the origin adds mechanism to a statistical model (see Cade and Terrell 1997 for ways to avoid this) and thus makes it an implicitly theoretical model. Often a good statistical model will identify relationships that then lead us to think about the mechanisms underlying them. Lanka et al. (1987), for example, found that geomorphic variables alone, used in a statistical (regression) model, predicted the standing stock of trout as accurately as stream habitat variables (see also Nelson et al. 1992). This presents a challenge to understand the mechanistic relationship underlying the statistical discovery.

To be sure, all kinds of models are needed for the solution of ecological problems. As theoretical models become larger and computationally more intensive, they require more parameters, and thus we end up with a hybrid between a theoretical and statistical model. Bartholow et al. (1993), for example, constructed such a model for spatially distinct cohorts of chinook salmon (*Oncorhynchus tshawytscha*). They used theoretical descriptions of life history characteristics and statistical descriptions of flow patterns of the Trinity River (see also Williamson et al. 1993). The fundamental notion here is that flow-dependent physical habitat and water temperature may either increase or limit the carrying capacity of streams. To operationalize this assumption requires careful use of theoretical and statistical models—and knowing which is which (see Gore et al. 1992; Harper et al. 1992; Kershner and Snider 1992). Baker and Coon (1997) used a theoretical model, based on optimal foraging theory, to evaluate habitat suitability criteria for brook trout (*Salvelinus fontinalis*).

To construct an effective model requires specification of mechanisms, processes, and parameters that may not be available. Models are tools to guide further inquiries in the laboratory, in the field, or in the literature (Gabriel 1993). They are not the truth, but they are “the lie that helps us see the truth” (Fagerström 1987).

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