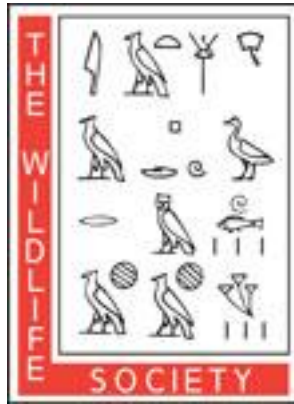


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## Habitat Evaluation: Do Use/Availability Data Reflect Carrying Capacity?

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# HABITAT EVALUATION: DO USE/AVAILABILITY DATA REFLECT CARRYING CAPACITY?

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**Abstract:** Evaluating the quality of habitat for wildlife is fundamentally important to decisions on land use. Habitat evaluation models are frequently based on the assumption that habitat use/availability data correspond in some fashion to the carrying capacities of habitats for populations and that the correspondence is independent of realized population density. We believe that assumption may be misleading whenever the quality of habitat resources is not directly related to their quantity. We use a simple model to illustrate that habitat use/availability ratios change as population density changes and may have no relation to carrying capacity when resource quality and quantity are not substitutable for one another. We advocate developing habitat evaluation systems that are based on a mechanistic understanding of relations between resource acquisition by individuals and the dynamics of populations.

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Quantitative evaluation of habitat for wildlife has emerged as an important component of land management planning. As a result, many habitat evaluation models have been developed. The predictions of those models influence decisions on land use involving millions of hectares annually. In most cases, carrying capacity (the capability of land to maintain and produce animals of a given species) is the stated or implied measure of habitat value (e.g., Flood et al. 1977, U.S. Fish Wildl. Serv. 1981, Cooperrider 1986, Verner et al. 1986). In the absence of direct measures of carrying capacity, many current habitat evaluation models rely heavily on habitat use/availability data, implicitly assuming that such data reflect the value of different habitat types for populations of animals. That assumption usually is based on the following reasoning: "It is assumed that (1) a species will select and use areas that are best able to satisfy its life requirements; and (2) as a result, greater use will occur in higher-quality habitat" (Schamberger and O'Neil 1986:9). Although there may be a logical relation between habitat preference and habitat quality at the level of the individual animal, the relation between habitat preference and carrying capacity at the level of the population is much less clear.

Habitat use and availability data attempt to reveal differences in the spatial distribution of animals as it is influenced by differences in vegetative cover, landform, and other features of the environments animals use. Animal distribution is the spatial expression of animal abundance (Andrewartha and Birch 1954:5-10). Thus, commonly used indices that express hab-

itat use (via radio locations, fecal indices, call counts, etc.) in ratio with habitat availability are inherently indices of spatial variation in population density (Fagen 1988).

Van Horne (1983), however, showed that indices of animal density will offer misleading conclusions about habitat value when social behavior excludes individuals from valuable habitats. She showed clearly that under such conditions animal densities may be inversely related to habitat quality (Van Horne 1982). Recently, Fagen (1988) dismissed the arguments of Van Horne (1983), viewing her results as a special case. Fagen (1988) contended that habitat value will be directly related to use/availability ratios whenever animals are free to choose the habitat that confers the greatest fitness. Specifically, he argued that when animal distributions are "ideal free" (sensu Fretwell and Lucas 1970, Fretwell 1972), the carrying capacities of habitats will be directly proportional to use/availability indices, regardless of when those indices are obtained.

Here, we offer simple graphical and numerical models to examine the relations among use/availability data, habitat quality, and carrying capacity. We apply the models to motivate a change of direction in studies designed to evaluate habitat for wildlife.

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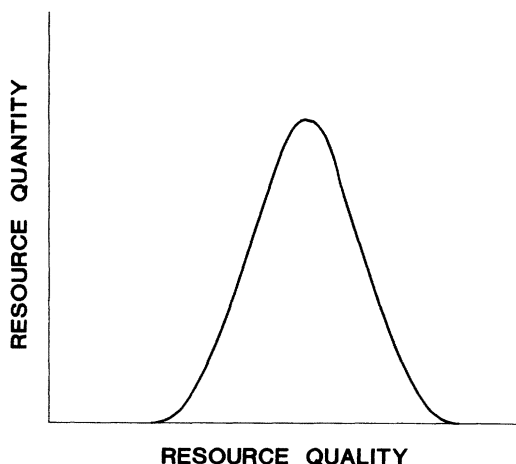


Fig. 1. Hypothetical resource distribution. The mass or frequency of a resource in a habitat is plotted as a function of its quality.

## APPROACH

### Graphical Model

We begin with 2 assumptions. Consistent with the approach of Fagen (1988), we assume that at any given time, empirical measures of habitat preference (e.g., use/availability measurements) reflect relative differences in population density among habitats. We assume further that limitations imposed by habitat resources on animal density can be described in at least 2 dimensions, a dimension defining the quantity of the resource and a dimension defining its quality. That is, we assume that both the quantity and quality of resources within a habitat determine natality ( $b_x$ ) and survival ( $l_x$ ) of animals using that habitat. We define resource quality such that higher quality allows greater  $l_x$  and/or  $b_x$  per unit of available resource.

We can characterize resources to include both quantity and quality dimensions by constructing a distribution that describes mass or frequency of a resource as a function of its quality (Fig. 1). For example, food supplies for herbivores can be represented as a resource distribution where the biomass of forage is a function of its nutritional value (Sibbald et al. 1979, Breman and de Wit 1983, Demment and Van Soest 1985, Hobbs and Swift 1985, Gordon 1989, Hanley and Rogers 1989, Hobbs 1989). Other examples of resource distributions within habitats might include the abundance of nest sites offering different levels of security from predators (Gates and Gysel 1978) or the spatial area of thermal cover providing different abilities to

mitigate heat or cold stress (Parker and Gillingham 1990). To simplify our explanations, we assume that only a single dimension of quality is operative here, but we acknowledge that multiple dimensions are probably important in nature (e.g., Hobbs 1989:Fig. 2).

Dimensions of quality and quantity that define resource distributions may or may not be substitutable. A substitutable distribution of resources is one where deficiencies in resource quality can be directly offset by an increased abundance of the resource. For example, a predator may be able to compensate for reductions in prey size by eating a large number of prey, an outcome that is possible if sufficient prey are available. In contrast, other resources lack substitutability between quantity and quality. For example, a ruminant cannot fully compensate for low dry-matter digestibility by eating more dry matter. A bird cannot compensate for inadequate nesting cover by using several nest sites. A fish cannot compensate for poorly oxygenated water by swimming in a bigger lake. In these cases where quantity cannot substitute for quality, increasing resource abundance merely reduces intraspecific competition for resources, but cannot make up for inherent deficiencies in those resources.

Consider 2 hypothetical resource distributions,  $\alpha$  and  $\beta$ , for which quantity and quality are not substitutable (Figs. 2A and 2B). In both cases the average quality of resource in  $\alpha$  is greater than in  $\beta$ . In 1 case, however, the total amount of resource (i.e., the area under the resource distribution curve) in  $\alpha$  is greater than in  $\beta$  (Fig. 2A), whereas in the other case, the amount of resource in  $\beta$  is greater than in  $\alpha$  (Fig. 2B). Assume that intraspecific competition for resources causes natality and survival of individual animals to increase asymptotically with increasing per capita amount of available resource and that the upper limit on natality and survival is set by resource quality (Fig. 2C). This immediately calls to mind a Type II functional response (Holling 1959), but we do not restrict our example to food; we consider any resource that affects an individual animal as in Figure 2C. Moreover, for our arguments here, the precise shape of this response does not matter as long as the product of  $b_x$  times  $l_x$  does not decrease with increasing resource amount at a given quality level.

The effect of resource quality is seen at the level of the individual animal. Resource distri-

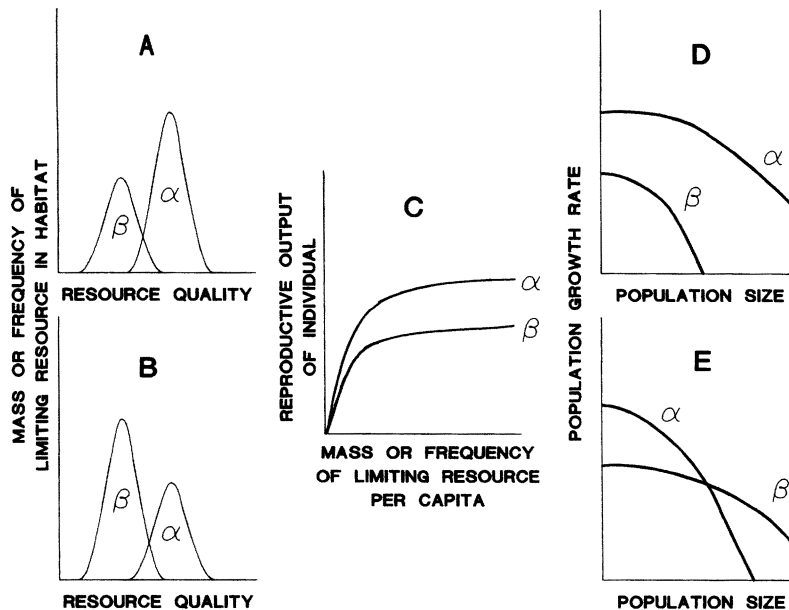


Fig. 2. Performance of individual animals and animal populations in 2 habitat types,  $\alpha$  and  $\beta$ , given different assumed resource distributions. A—Quality and quantity of resources in  $\alpha > \beta$ . B—Quality of resources in  $\alpha > \beta$  but quantity of resources in  $\alpha < \beta$ . C—Reproductive output of individuals is determined by resource quality when per capita availability of resources is identical between  $\alpha$  and  $\beta$ . D—When quantity and quality of resources are greater in  $\alpha$ , then individual reproductive output and population growth in  $\alpha$  exceed growth in  $\beta$  at all population densities. E—When quantity of resources is greater in  $\beta$ , but quality is greater in  $\alpha$ , then the ranking of individual reproductive output and population growth depends on population density.

butions  $\alpha$  and  $\beta$  will produce different net reproductive outputs when the same quantity of resource is available to an individual in each habitat. It follows from our definition of resource quality that if the quality of  $\alpha$  is greater than  $\beta$ , the functional relationships between reproductive output and per capita availability will never intersect (Fig. 2C). That is, when comparing 2 animals experiencing identical quantity of resources in habitats  $\alpha$  and  $\beta$ , the animal in  $\alpha$  will always leave more descendants because of the quality advantage offered by the resources in  $\alpha$  (Fig. 2C).

The effect of resource quantity is most pronounced at the level of the population. First, consider the case when the quantity of resource in  $\alpha$  is greater than in  $\beta$  (Fig. 2A). Given populations of identical size, the population in  $\alpha$  will always have a higher growth rate because, on average, individuals in  $\alpha$  will have greater  $l_x$  or  $b_x$  (Fig. 2D). The net reproductive output of individuals in  $\alpha$  will exceed that in  $\beta$  because at any given population size the quantity of resources experienced by individuals in  $\alpha$  will never be less than in  $\beta$ , and the quality experienced will on average be greater.

This will not be the case, however, when the amount of resource in  $\beta$  is greater than in  $\alpha$  (Fig. 2B). In that case, there is a trade-off between quantity and quality. At any given population size, the per capita amount of resource in  $\alpha$  is less than in  $\beta$  (i.e., the population in  $\alpha$  will be further to the left on the x-axis in Fig. 2C). It follows that individual reproductive output in  $\beta$  can exceed that in  $\alpha$  when populations are sufficiently large. Hence, curves for individual reproductive output as a function of population size can intersect (Fig. 2E). When the amount of resource in  $\alpha$  is less than in  $\beta$ , but the quality of resource in  $\alpha$  is greater than in  $\beta$ , then individual reproductive rates and population growth can be greater in  $\alpha$  than in  $\beta$  when populations are small, but less when they are large. Whether this occurs depends on the precise relations between resource quantity and quality as they affect reproduction and survival. Here, we simply make the point that such intersections are plausible outcomes in nature.

### Simulation Model

We now use those relations in a simple age-structured population dynamics model to link

Table 1. Parameters and their values defining population behavior in 2 habitat types, one with a small amount of high quality resources ( $\alpha$ ), the other with a large amount of low quality resources ( $\beta$ ).

Parameter	Definition	Habitat	
		$\alpha$	$\beta$
$l_x^a$	Survival rate of all age classes	0.90	0.90
$r$	Maximum natality rate of all age classes (F produced/ad F)	0.60	0.20
$\theta$	Rate constant specifying per capita food biomass at which natality = $r/2$	60	60
$NPP$	Annual food production	1,000	10,000
$P$	% of total area in each habitat	50	50

<sup>a</sup> In I scenario, survival rate was variable.

the ideas with the concept of equilibrium density, or carrying capacity. We will illustrate that “habitat preferences” measured by use/availability data may be unrelated to habitat carrying capacities when there is a trade-off between the quality and quantity of resources limiting population growth.

**Model Description.**—The model is structured as a Leslie Matrix (Leslie 1945) and is intended to represent a vertebrate population limited by its food supply. It runs at a 1-year time step. For simplicity, annual food production is considered to be constant. The modeled population contains 12 age classes. We assume that no animals live longer than 12 years and that  $l_x = 0.9$  for animals until age 12.

We represent the effects of intraspecific competition for food as follows. As the amount of food per capita declines, natality diminishes at an accelerating rate,  $b_x = [r(NPP/N)]/[(NPP/N) - \theta]$ , where  $b_x$  = realized natality rate (No. F produced/F),  $r$  = maximum natality rate (No. F produced/F) permitted by resources of a given quality,  $NPP$  = annual food amount available to the population,  $N$  = population size, and  $\theta$  = rate constant (the value of  $NPP/N$  where  $b_x = r/2$ ). Thus, the natality rate in the model is controlled as in Figure 2C.

**Model Experiments.**—To examine the relation between use/availability data and carrying capacity, we used the model to represent population growth in 2 habitats,  $\alpha$  and  $\beta$ , with resource distributions as in Figure 2B. Values for model parameters representing the 2 habitats are given in Table 1. We assumed that the 2 habitats were equal in size, and we calculated use/availability indices as  $N/P$ , where  $N$  is the total population size and  $P$  is the percentage of each habitat in the total available habitat. We defined carrying capacity as the population size for which the population growth rate is zero.

We ran 4 100-year simulations, each representing a specific scenario. In scenario A, we ran the model under the assumption of no interchange between habitats  $\alpha$  and  $\beta$  to illustrate the underlying dynamics of populations in the 2 habitats. In scenario B, following Fagen (1988), we assumed an ideal free distribution of animals. In those simulations, animals used habitat  $\alpha$  exclusively when natality rate in  $\alpha$  was greater than in  $\beta$ , but when natality in  $\alpha$  was less than in  $\beta$ , animals migrated from  $\alpha$  to  $\beta$  until natality rates in the 2 habitats were identical. In scenario C, we added stochastic variation in survival by adding a rule to the model specifying that during any year chances were 1 in 10 that survival of all animals would drop from 0.9 to 0.8. Finally, in scenario D, we created a new habitat patch ( $\pi$ ) during Year 50 of the simulation and allowed ideal free emigration to that patch. Model parameters for habitat  $\pi$  were set to those of habitat  $\alpha$  in Year zero. For all simulations, we observed trajectories of population growth and changes in ratios of habitat use/availability.

RESULTS

Given the assumption of no dispersal between habitats (scenario A), trajectories of population growth in habitats  $\alpha$  and  $\beta$  showed clear equilibrium densities (Fig. 3A). Carrying capacity of habitat  $\alpha$  was 55 animals; carrying capacity of habitat  $\beta$  was 72 animals. When we assumed that the distribution of animals followed ideal free rules (scenario B), habitat  $\beta$  was unoccupied until year 8, at which time the achieved natality rate in habitat  $\alpha$  fell below the possible natality rate in  $\beta$ , thereby stimulating migration from  $\alpha$  to  $\beta$  (Fig. 3B). During the first 22 years of the simulation, habitat use/availability indices revealed  $\alpha$  to be the “better” habitat. During later years of the simulation,  $\beta$  showed higher use relative to availability. It follows that inferences

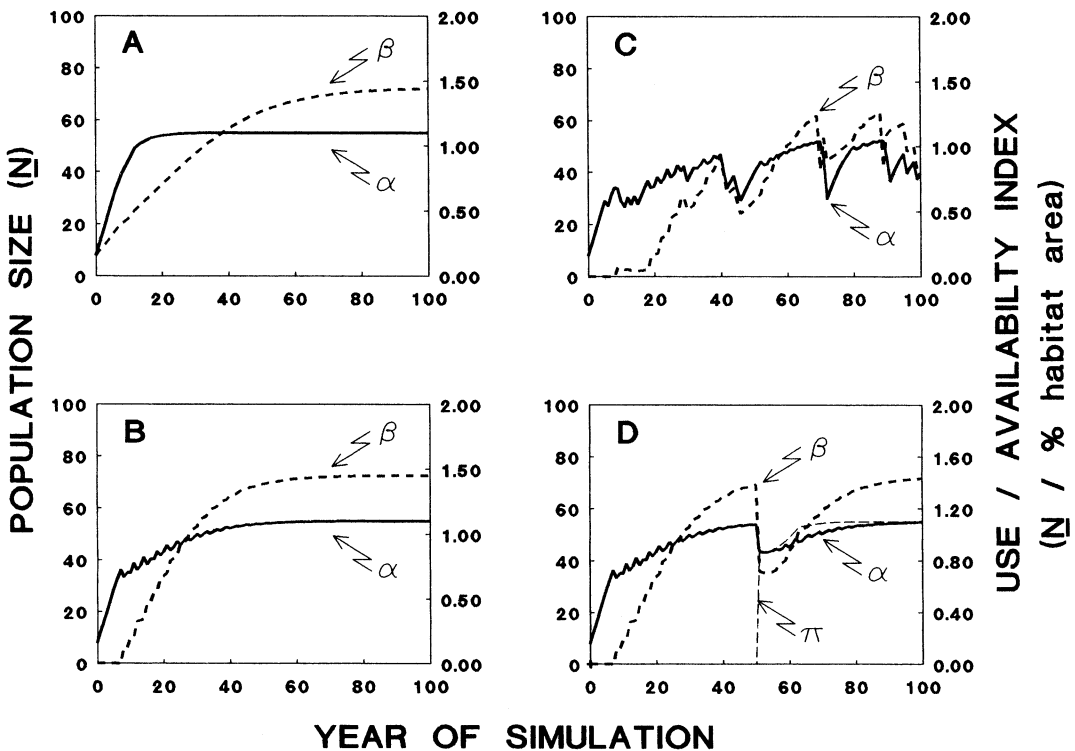


Fig. 3. Model simulations of temporal changes in population size and habitat use/availability indices. Letters correspond to model scenarios. Assumptions for each population scenario were as follows: A—No interchange between habitats and constant survival. B—Ideal free distribution between habitats and constant survival. C—Ideal free distribution and stochastic variation in survival. During any year survival could be 0.90 (with a probability of 0.90) or could be 0.80 (with a probability of 0.10). D—Ideal free distribution with a third habitat patch ( $\pi$ ) created during Year 50. Habitat parameters of  $\pi$  were set to those of  $\alpha$  in Year 0; survival was assumed constant.

on habitat value derived from use/availability indices depended on the year those indices were obtained. Moreover, contrary to Fagen (1988), there was no predictable relation between habitat use/availability data and carrying capacity.

If one assumes an ideal free spatial distribution of animals and that equilibrium densities in populations prevail over time, then use/availability indices will be proportional to carrying capacity (Fig. 3B). However, events that deflect populations from equilibrium will make that proportionality less likely in nature. For example, density-independent perturbations in survival (scenario C) caused unforeseeable changes in the relation between simulated availability-use data and carrying capacity (Fig. 3C). Small and infrequent changes in survival caused large temporal variation in simulated habitat use/availability indices. Although there were long time intervals (about 10 yr) during which use/availability data would indicate that 1 hab-

itat was more valuable than another, the rankings shifted unpredictably.

Similarly, when we structured our simulations such that new habitat was created outside the boundaries of  $\alpha$  and  $\beta$  habitats (scenario D), the resulting shifts in ideal free distributions caused the ranking of habitats based on use/availability data to change with time (Fig. 3D). Scenario D illustrated that habitat use/availability ratios are not comparable over time even when population densities remain constant. Calculating the ratios before Year 50 (when there were 2 habitat patches) required dividing population numbers by 50%, after Year 50 by 33%. Thus, even when animal numbers within habitats remain unchanged, habitat use/availability indices will shift as new habitats are created or removed.

## DISCUSSION

The relation between the quality and quantity of habitat resources mediates interactions

among habitat carrying capacity, habitat preference, and population density. Taken together, our simulations (Fig. 3) illustrate that animal distributions will reflect habitat carrying capacities only when (1) animals are spatially distributed in an ideal free manner, (2) environmental conditions permit long-term, stable equilibria between animal populations and limiting resources, and (3) use/availability data are obtained after equilibria are achieved. Do those conditions prevail in nature? The ideal free distribution (Fretwell and Lucas 1970) should be viewed as a theoretical construct rather than a realistic rule describing habitat selection (Fretwell 1972). Moreover, evidence is accumulating that equilibrium conditions may be relatively rare in many populations of vertebrates (Wiens 1977, Huston 1979, Wiens and Rotenberry 1981). Given the importance of natural and man-caused disturbance in creating temporal variation in the relations between animal populations and their habitats (Pickett and White 1985, Turner 1987), we argue that the above assumptions will be rarely satisfied.

Although our results are based on a highly simplified model, adding complexity to simulated interactions between animals and habitats made the relation between habitat use/availability and carrying capacity increasingly tenuous. Our results are congruent with those of Fahrig and Paloheimo (1988), whose simulations revealed that carrying capacities of habitat patches were unrelated to population densities of animals using those patches. Instead, the ability of animals to disperse and their ability to detect new habitats emerged as important regulators of realized population densities.

We believe the conclusions from our model have parallels in nature. For example, Hobbs and Swift (1985) showed empirically that recently burned mountain shrub communities offered small amounts of extremely high quality food to mule deer, while unburned communities offered large quantities of relatively poor food. Consequently, the carrying capacities of the 2 habitats were inversely related to the achieved nutritional status of individual animals and, presumably, to the reproductive output of individuals using those habitats (Hobbs and Spowart 1984, Hobbs and Swift 1985). Burned areas could support a small number of well-nourished animals, but unburned areas could support far more animals at a lower level of condition. Thus, at

low population density, an individual deer would benefit substantially from feeding in the burned area. At high densities, however, the food supplies in burned communities would be rapidly exhausted while unburned ones would provide sustained nutritional benefits. Given such differences in resource distributions, we argue that the preference of individuals for habitats will change as population density changes. Predictions of models based on habitat matching rules (Fagen 1988) will be insensitive to those changes, and consequently will offer misleading conclusions.

Use/availability data inherently reflect differences in animal density among habitats (Fagen 1988). Our simulations amplify the caution of Van Horne (1983) that indices of animal density offer unsound conclusions on habitat value. Contrary to Fagen (1988), this result does not depend on assumptions about animal social behavior. Even when assumptions of ideal free distributions are met, observations of patterns of habitat use may be unrelated to rates of population increase or to equilibrium densities. It follows that short-term measures of habitat use/availability will reveal little about the value of habitat unless the underlying resource distributions limiting population growth are understood mechanistically. In evaluating habitats and in predicting the consequences of habitat change, however, such a mechanistic understanding makes the need for applying use/availability data unnecessary in the first place.

We suggest that future approaches to habitat evaluation should focus on mechanisms linking the performance of animal populations to resources in the habitats they use. Our suggestion is based on 2 lines of reasoning. First, habitat evaluation must be related to some objective for habitat. In our example simulations, habitat  $\alpha$  offered the greatest population growth rates, habitat  $\beta$  the greatest equilibrium density. Which is better? By definition, evaluation is a judgment of worth. No matter how quantitative our appraisal of habitat characteristics may be, comparisons of the worth of 1 habitat relative to another only have meaning in reference to some achieved result and the values we place on it. Is a habitat more valuable if it supports a larger standing crop of animals? Provides greater yield? Supports the more diverse fauna? Allows the greater stability in animal numbers? Is more representative of historical conditions? The rel-

ative value of a habitat changes as we change the standards of evaluation. Linking characteristics of habitats to objectives for populations can be achieved only when we understand the mechanistic relationship between those characteristics and the desired behavior in the animal population.

Our second line of reasoning emphasizes the importance of prediction in habitat evaluation. It is sometimes possible to evaluate habitats relative to some objective by carefully observing the performance of populations using those habitats and correlating animal performance with habitat characteristics. Such a retrospective, descriptive approach requires no understanding of the processes controlling population behavior. Retrospective analyses of habitat relationships depend on the conditions prevailing when the analyses were conducted, however, and offer no predictive value when those conditions shift (Rotenberry 1986). In prospect, habitat evaluation systems capable of predicting the effects of human impacts or other forms of disturbance require understanding the mechanisms by which the environment influences the distribution and abundance of animals. Forecasting the consequences of habitat change depends on understanding the processes that control animal response to change.

We do not yet have a scientifically sound and complete method of evaluating habitat quality. But Van Horne's (1983) analysis of density as an indicator of habitat quality and our analysis of habitat preference as an indicator of carrying capacity compel similar conclusions. An understanding of the cause-and-effect relations linking the performance of animal populations to the resources in their habitats is fundamentally important to evaluating habitat. Correlations based on simple surrogate variables (e.g., density, habitat use/availability indices) offer unreliable inferences on habitat value.

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## MANAGEMENT IMPLICATIONS OF FORAGING THEORY: EVALUATING DEER SUPPLEMENTAL FEEDING

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**Abstract:** I conducted an experiment in a northern deer yard to compare the foraging behavior of naturally wintering and supplementally fed white-tailed deer (*Odocoileus virginianus*) and to assess when supplemental feeding might be warranted. Deer survived on natural browse in 1 area of the yard and were provided ad libitum supplemental feed in another. I examined the effects of browse depletion and accumulating snow on diet selection in 3 winter sampling periods. I used an optimal foraging model to predict the diet for 2 potential strategies: (1) energy maximization, where deer maximize their energy intake to maximize survivorship, and (2) time minimization, where deer satisfy energy needs in the least feeding time thereby minimizing exposure to deleterious climate. Deer selected energy maximizing diets in all time periods and feeding areas. Naturally wintering deer were expected to select a mixed diet of coniferous and deciduous browse. Predicted diets (deciduous:conifer) for the 3 time periods were 1,130:46, 780:330, and 589:462 g dry mass per day. Observed diets for the same time periods were 1,090:65, 684:317, and 452:490 g dry mass per day. Naturally wintering deer satisfied requirements for survival, so supplemental feed was not required for winter conditions during the study. Supplementally fed deer were expected to eat only supplemental feed in all sampling periods. Contrary to predictions, they continued to eat browse. A sensitivity analysis, used to examine the reliability of model predictions because of variable parameter estimates, indicated the model predictions were robust. Thus, I concluded that the supplemental feeding program may have been inefficient. Supplemental feed was delivered in a few large feeders, which created a limiting resource. This probably increased competition at feeders, forcing individuals to browse.

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Winter in northern latitudes is considered stressful for deer because cold climatic conditions increase the energetic cost of survival (Moen 1978, Parker et al. 1984, Verme and Ullrey 1984). Moreover, food quality and abundance tend to be low (Moen 1978, Parker et al. 1984), so deer

may not obtain sufficient nutrients to satisfy survival requirements. Supplemental feeding programs have been initiated during winter to enhance the survivorship of deer (Mautz 1978a). However, managers often introduce these programs without evaluating whether they are necessary and/or efficient. To do so requires comparing the diets of naturally wintering and supplementally fed deer.

It is not sufficient, however, to simply compile lists of the taxonomic and nutritional differences

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