Chapter 2

Methods and Terminology Used With Studies of Habitat Associations

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The forest owl conservation assessments emphasize the relationship between flammulated, boreal, and great gray owls and the forests in which they occur. The habitat requirements of the owls and their principal prey bear strongly on the conservation status of the owls. Establishing the characteristics of the owl/habitat relationship is not a trivial or straightforward process. This discussion provides background on the study of habitat associations that will place the literature on owl habitat in theoretical perspective.

AN APPROACH TO ASSESSING HABITAT REQUIREMENTS

Habitat loss or degradation is a major threat to wildlife populations. Understanding the habitat requirements of a species is, therefore, critical to assessing its conservation status. Unfortunately, although the data gathered in most habitat studies may be useful, their actual analysis and interpretation are often flawed. Here I discuss habitat selection and methodology of habitat evaluation as a preamble to our analysis of existing information on the habitat of flammulated, boreal, and great gray owls.

In discussing habitat associations we must distinguish between habitat requirements, habitat preferences, and habitat use (occupancy). Habitat requirements are of greatest importance because they determine the fate of the population. They are, however, the most difficult habitat relations to resolve because they require estimation of a complex fitness function (figure 1). Habitat preferences, which may not be identical with requirements (Lack 1933), are best discerned through experimentation, although carefully designed statistical tests can reveal some aspects of preferences. Occupancy is simple to measure but can be misleading, particularly when occupancy is weighted by abundance of the target species. Each of these points is amplified below.

HABITAT REQUIREMENTS

Habitat requirements are revealed by the relationship between fitness and a habitat gradient (figure 1). Fitness, or some proxy for it, can in principle be measured along any such habitat gradient. The methods used to choose the gradient and to measure fitness are of great practical importance but do not influence the underlying logic discussed here. Various methods for measuring habitat use and availability, and their shortcomings, are discussed in detail by Morrison *et al.* (1992).

The habitat-specific fitness function can be uniform (identical fitness associated with all values along the habitat gradient) but is likely to be irregular in shape (e.g., figure 1). Fitness is influenced not only by the physical and structural features of the habitat gradient, but also by the biota that occupy some or all of it. This fact makes uniform fitness functions extremely unlikely in nature.

The points at which individuals can neither survive nor reproduce (figure 1) define the extremes of the "range of tolerance" of the species along that habitat gradient. A horizontal line, representing the fitness at which the population replaces itself but does not increase ($\lambda = 1$ or $r = 0$), cuts the fitness function at habitat values that define the boundaries between source and sink habitats. Sink habitat is defined as habitat in which individuals can survive and reproduce, but not at rates sufficient to maintain the population without immigration. The source-sink concept (Lidicker 1975) is familiar, but its relevance to conservation biology in general (Pulliam 1988), and to habitat evaluation in particular, has been overlooked.

A fitness function can be written for a single genotype or for an entire (genetically polymorphic) population. If the fitness function is for a single genotype, its maximum identifies the optimal habitat for that genotype, unless the replacement line is irregular (i.e., fitness required for replacement is not independent of habitat type), in which case the optimal habitat is indicated by the maximal positive difference between fitness and the replacement line.

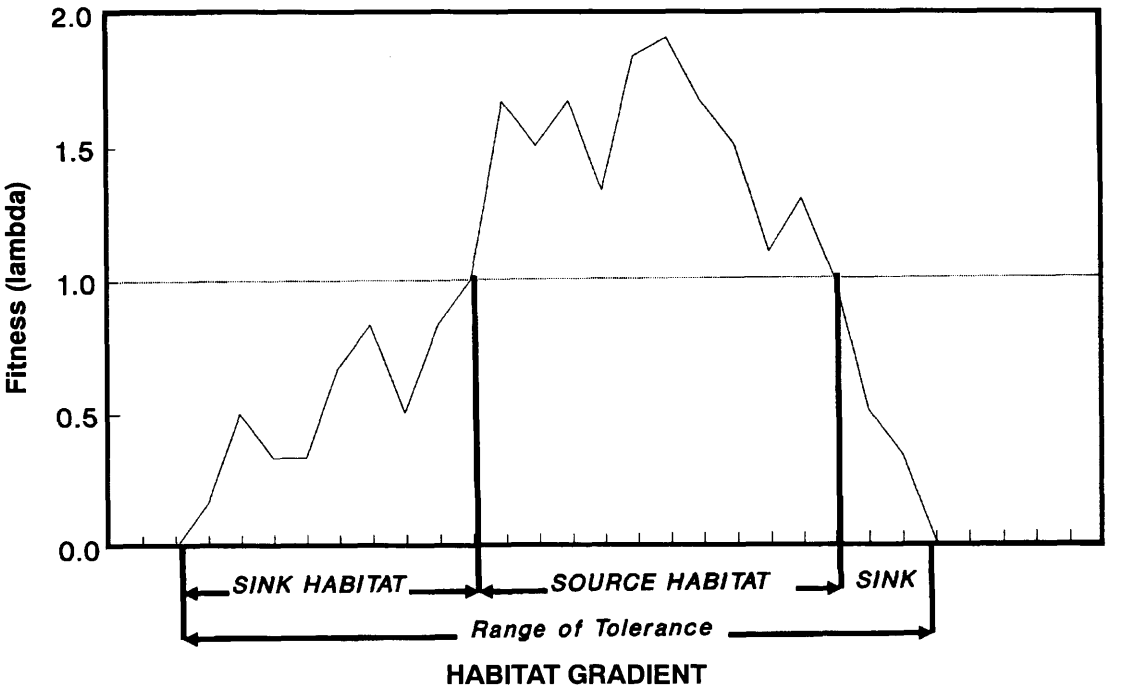

Figure 1.—Fitness (geometric rate of natural increase, λ) in relation to a habitat gradient. Growing populations (λ > 1) are sources of individuals for populations in habitat not capable of sustaining a stable population (sinks, λ < 1). All occupied habitats are within the range of tolerance.

If, however, the fitness function is a composite of the fitness functions of different genotypes, which is probably the case in most wildlife populations, it represents the weighted mean fitness of all genotypes occurring at each point on the habitat gradient. In this case, the maximum of the fitness function is controlled by the relative abundance of the various genotypes and indicates optimal habitat for the population, given the current mix of genotypes in the population.

Determination of fitness functions specific to genotypes requires genetic markers; determination of a composite fitness function requires only an adequate random sample of individuals occupying the gradient. Estimating the vital rates (e.g., fertility and mortality) required to write a fitness function can be extremely time-consuming, especially if they vary with age. Estimation of rates of survival from fledging to the age at which breeding begins is complicated by the difficulty of estimating rates of successful natal dispersal.

Habitat-specific fitness functions are critical to assessing habitat requirements because fitness is a direct measure of how well adapted a population is to a particular environment at a particular time. An accurate fitness function tells how well a population exploits different environments and thereby indicates which environments will best support the species in the long term. (It is nonetheless applicable only to the population for which it was measured.) Measures such as population density, habitat use, and even habitat preference are proxies and are unneeded if fitness is truly known. If not interpreted carefully and cautiously, these proxies can be misleading.

HABITAT PREFERENCES

All treatments of habitat selection in birds assume selection is at least in part active; birds seek habitats on the basis of internalized standards (e.g., Lack 1933), rather than passively accepting random locations and then making the best of them. Active selectors necessarily have a preference function, i.e., a set of standards of desirability (preference) for different values of a habitat gradient. Accepting existence of a preference function in no way implies an assumption of consciousness on the part of the animal.

Such a preference function is potentially different from the fitness function along the same gradient because the genes (Jaenike and Holt 1991) and the learning that underlies the behavior necessary to find a site are not necessarily those underlying its optimal exploitation. The most preferred habitat can be sink habitat if evolution of the preference function lags behind evolution of the habitat-specific fitness function when the latter is changing rapidly, as when

natural selection is severe following a catastrophic change in the availability of habitat types or the invasion of a region by a superior competitor or predator (Van Horne 1983). One would expect natural selection to bring the two functions back into phase (Jaenike and Holt 1991). For the sake of simplicity, I will assume hereafter that the preference function accurately reflects the fitness function.

Aspects of preference can be identified by examining the relationship between occupancy and availability of habitat, but great care must be taken in interpreting such relationships because occupancy does not equal preference. Preferred habitat may not be available; occupied habitat and preferred habitat may therefore differ. It follows that occupancy patterns in some populations may actually obscure the true habitat requirements of the species because the individuals are merely doing the best they can under bad circumstances. Individuals will manifest preferences among available habitats as long as they have choice, even if all their options are suboptimal.

HABITAT SELECTION AND OCCUPANCY

Habitat selection is the process whereby preference is translated into occupancy. In classical habitat-selection theory (Fretwell and Lucas 1969, Fretwell 1972) and modern expansions of it (e.g., Pulliam and Caraco 1984, Pulliam 1988), individual animals assess habitat and settle where their potential fitness is highest. No one assumes that they actually calculate fitness. Rather, these models assume that internalized preferences, either innate or as templates subject to modification by learning (e.g., habitat imprinting), dictate the choice.

Habitat selection theory tends to focus on a single habitat dimension. But habitat preferences do not exist in a vacuum. Rather, they coexist with preferences on other habitat dimensions and at other spatial (e.g., nest-site and foraging range) and temporal (e.g., foraging and roosting) scales. Thus an individual may occupy suboptimal habitat on one dimension because of an absolute requirement on another dimension. An obvious example is that flammulated owls cannot nest in home ranges with high quality foraging habitat if no cavities exist there.

The habitat an individual actually occupies is influenced by the preference functions specific to its genotype, *and* by the availability of that habitat. Availability is a function of both the abundance of the habitat within the searching range of the would-be occupant *and* the number of individuals already occupying it. Interspecific competition and/or the danger of predation may also force individuals to occupy suboptimal sites.

Because habitat occupancy is a function of *both preference and availability*, preference cannot be inferred from occupancy without also considering availability. According to the theory summarized above, densely occupied areas could be sink habitat (figure 1), which late-arriving or inferior competitors occupy temporarily while waiting for the opportunity to move into higher quality, preferred habitat. Sink habitat may be densely occupied because source habitat is producing a large surplus of individuals (e.g., Krebs 1971), which may mean that the population has an excellent probability of long-term persistence. Or, more ominously, sink habitat may be densely occupied because source habitat is rare but productive. In this case the sustainable population size is lower than the actual size and dependent upon the rare source habitat. If source habitat has recently been reduced in extent, a decline to a new and lower equilibrial population size can be expected, despite the current abundance of birds in the sinks. Obviously, abundance is not an infallible indication of habitat quality (Van Horne 1983, Vickery *et al.* 1992a,b).

It is possible, however, to make some valid inferences about habitat preference with a comparison of habitat occupancy and habitat availability (provided these can be measured accurately; see Morrison *et al.* 1992). The first step is to confirm that selection has taken place. A statistical test is used to test for differences between observed occupancy patterns and expected occupancy patterns under an assumption of random settlement. The expected pattern is given by the actual availability pattern. A significant difference indicates that settlement was nonrandom. Nonrandom settlement is habitat selection (active or passive). This statistical procedure tests the hypothesis that the species selects habitat along the gradient in question. It confirms that preference is manifested, but the statistical test itself does not identify the preference.

For example, it might be shown that the mean value of canopy coverage in occupied sites is significantly less than the mean value in all sites (or unoccupied sites). This shows that the birds have selected sites with respect to canopy coverage (or some factor correlated with it), and it suggests that they prefer relatively open sites (within the range of available structures), but it does not say that the mean canopy coverage of occupied sites is the value preferred by these birds. The most preferred condition may not even be available in the area sampled.

The second step is to inspect the data in an attempt to infer preferences. (This inference, of course, is

valid only for the population on which it is based. Extrapolation to other populations is not valid, because fitness and preference functions are context-specific.) The inference can be strengthened with information on the degree of habitat saturation. If the habitat is not saturated, occupied sites are likely to be the most highly preferred of those available. This inference is based on the assumption that each bird will occupy the site it prefers most, among the sites available to it (Alatalo *et al.* 1985). If the habitat is saturated (which itself is difficult to assess), then preferred habitat will not be revealed by comparing occupancy and availability. The extreme values of the occupancy pattern may well indicate the boundary between totally unsuitable and minimally acceptable sites (e.g., the dimensions of a nest cavity entrance would have such a minimum). Notice that "totally unsuitable" and "sink habitat" are not synonymous. In other words, saturated occupancy distributions may reveal the limits of tolerance of a species along a habitat gradient but can reveal little about optimal habitat.

This entire discussion has been focused on territorial species in which individuals can control territories and preserve the fitness differentials between them and lower quality habitat. In the limit, as intruder pressure reaches a level that makes territory defense uneconomical for the defender, territoriality will break down. At this point intruders should distribute themselves to maximize their individual expected fitness, with average fitness being equal across the habitat gradient once an equilibrium is reached. This special case, referred to as the ideal free distribution by Fretwell (Fretwell and Lucas 1969, Fretwell 1972), is a situation in which local density is an accurate indicator of habitat quaiity.

Interpretations of habitat occupancy patterns are hypotheses about the preferences of the species in question along the habitat gradient in question. Ideally such hypotheses should be tested experimentally to confirm that they have accurately identified the preferences of the population.

Keeping in mind the distinctions among fitness, preference, and occupancy should facilitate evaluation of published accounts of owl habitat use, most of which are anecdotal or qualitative assessments of habitat occupancy. In most cases occupancy patterns only suggest hypotheses about the habitat requirements of the species, but such hypotheses are useful in planning future research and current management.

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