Northwest Science Forum

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On the Limitations of Species-Habitat Association Studies

A trend in wildlife ecology over the last 25 years has been to study characteristics of a species habitat, primarily vertebrate species of management concern, and then infer something about habitat *preferences* or *suitability* for that particular species (e.g. Verner *et al.* 1986). The approach includes identifying a relatively high density population of a given species, or in some cases documenting the home ranges of representative individuals from that population, and then correlating habitat use or daily activity patterns with a series of habitat measurements such as plant species composition, vegetation juxtaposition, topography, and so forth. Presumably, this correlation tells something about habitat preferences or suitability for the species. In many cases, the study stops here and is published simply with correlational results. More appropriately, the correlational results are used in wildlife-habitat association or habitat suitability index (HSI) models (Fish and Wildlife Service 1981; Verner *et al.* 1986). These models have their application if tested properly, but they too have their pitfalls and shortcomings (e.g. Laymon and Barrett 1986; and other references in Verner *et al.* 1986). Herein, I summarize what I see as some problems associated with the use of wildlife-habitat association studies as endpoints in themselves. I am not the first to point these out and I refer the reader to Ruggiero *et al.* (1988) and many of the references in Verner *et al.* (1986) and Morrison *et al.* (1992) for further discussion. My arguments are of a general nature and I avoid citing specific studies to make a point. My intention is not to denounce all habitat-association studies, but rather to caution investigators and managers of their pitfalls and limitations. In doing so, I emphasize the importance of understanding behavioral as well as ecological factors that determine a species distribution.

1. The wildlife-habitat correlational approach does not provide an endpoint in itself. Wildlife habitat association studies are conducted where a species is known to occur; therefore, some positive correlations are likely to be derived for that species and some particular habitat feature(s). This type of study provides only the baseline data necessary to predict where a species *can* occur. Two additional components are required to make the study conclusive and the results predictive. First, to verify the relevance of these habitat correlates to the presence of the species, the study must document that the species does not occur in other randomly selected areas where these habitat features do not exist. Second, the study must test the now *a priori* predictions that the species will occur in habitats where these features are present and not in areas where they are not (i.e. the retrospective correlational study now becomes prospective). This

testing of the model can be done through natural experiments by finding similar habitats that do and do not have these same key features or through manipulation and experimentation (see references in Verner *et al.* 1986 for results of attempts to validate models). This last part of the study, and in some cases the latter two parts, are often not done. Therefore, the species-habitat correlation part of the study is left incomplete. Without the latter two parts the study, managers can not make defensible predictions or conclusions, or have confidence in management decisions. I might point out that management agencies are very good at funding the first of the series, but almost never fund the validation studies. The lack of validation causes uncertainty and may ultimately result in loss of credibility of biologists.

2. Species ranges of tolerance are often greater than can be measured in one short-term localized study. The historic distribution records of vertebrate species shows that most species at one time had much greater ranges than they have today. Most species of management concern have a much wider range of ecological tolerances than can be described in one isolated subpopulation. We also know that many of these species live in a variety of macro- and microhabitats (consider for example the variety of habitats in which elk, *Cervus elaphus*, marten, *Martes americana*, Douglas squirrels, *Tamiasciurus douglasii*, and red-tailed hawks, *Buteo jamaicencis*, occur). Therefore, species-habitat correlations determined from only a few individuals from a subpopulation in a small part of the species range tells us virtually nothing about the range of tolerance for that species throughout its distribution. In this sense, species-habitat association studies are not species-level studies, but rather subpopulation-level studies. Species obviously survive very well outside the range of any habitat measurements made in a specific subpopulation-habitat association study. Thus, the results may be relevant for the particular study site examined and not much beyond that (but see Noon *et al.* 1980). The result, therefore, has little, if any, predictive power for the species, yet is often accepted as factual and conclusive and applied to the species in other parts of its range. This may be an inappropriate application of these results, especially for species with wide distributions that exhibit ecotypic variation which may or may not be genetic adaptations to localized conditions.

3. The results from species-habitat association studies are often interpreted to mean that the species does not or cannot exist in areas where these selected habitat features do not exist. In other words, presumably all the "good" habitat is utilized and to increase numbers of individuals or population size, more of this good habitat should be created. This may not be a valid assumption for at least two reasons. First, many species now survive in refugia habitat that remains after humans exploited much of the habitat previously occupied by the species. Therefore, a given species may be existing in marginal and not optimal habitat, because optimal habitat no longer exists. Second, consider for example the Ideal Free Distribution Model of Fretwell and Lucas (1970) which proposes that animals first settle in "optimal" habitats and then as these territories become occupied, additional individuals settle in "suboptimal" or "marginal" areas. The reproductive success of individuals in suboptimal or marginal areas may be just as good as those in optimal areas for a variety of reasons. On the other hand, the Ideal Dominance Distribution (Fretwell 1972) and Source-Sink Models (Wolff 1982, Pulliam and Danielson 1991) do have survival and fitness consequences for individuals in optimal, suboptimal, and marginal habitats. Some measure of fitness is thus necessary to conclude something about habitat quality (see also number 10 below). Similarly, species-habitat association measurements focus on a very short-term time frame, often less than one year, and do not consider multi-annual, or in some cases even seasonal variation in habitat use, or lifespan of the species (voles, *Microtus*, versus elephants, *Loxodonta*, versus migratory caribou, *Rangifer tarandus*).

A related assumption often made in species-habitat association studies is that the population is at carrying capacity, in "optimal" habitat, and is relatively constant in time and space. This assumption too is often invalid and probably never tested. For instance, habitat and(or) nest-site selection may vary temporally and spatially especially for predators that feed on fluctuating prey such as lemmings, *Lemmus lemmus*, or snowshoe hares, *Lepus americanus*, or for nesting birds in the presence or absence of predators. A perfect or even "optimal" habitat probably does not exist for any species, but rather most species are flexible in their requirements and adjust to variable ecological conditions. Habitat association studies should focus

more on the limitations for a given species than on studying populations where they do "best." Limitations as well as "best" must be defined in terms of survival and reproductive success.

4. A problem exists with independence of observations and lack of replication. Although some studies have used replicate plots that are independent of each other, most studies use individuals rather than plots as replicates. In the case of social animals such as deer, *Odocoileus* sp., and elk, the movements and habitat use of one individual are not independent of those of another individual in the same social unit, such as a mated pair, mother and offspring, or members of the same harem. In territorial species, the position of each territory is influenced by the boundary of an adjacent individual (i.e. no two individuals can occupy the "preferred" space). In mammals, the space used by males may be more dependent on the spacing of females than any specific habitat feature. For large herbivores such as deer, elk, and caribou, males associate with females only during a short breeding season, whereas during the nonbreeding season, the sexes are segregated, often in very distinct habitats. In small mammals with long breeding seasons, males select habitat based on the proximity of estrus females. In birds, males establish territories and females choose males based on their territory. Therefore, habitat selection or preferences of males and females that have contiguous or overlapping home ranges are not independent of each other and can not be used as independent observations for statistical purposes. Similarly, for species that exhibit seasonal segregation of the sexes, each sex, habitat, and season must be considered separately. This is rarely done.

5. What does "habitat preference" really mean to the individual animal. Just because an individual spends more time in one habitat than expected, based on the habitat's frequency of occurrence (= preference), says nothing about how critical that habitat is for survival and reproduction. For instance, marten spend 95% of their time in forest habitat, but a very critical 5% of their time hunting voles in adjacent grassland habitat (Spencer 1981; Zielinski 1981). Likewise, many owls require large trees for nesting and adjacent open fields for foraging. Therefore, habitat requirements may include a mosaic of habitat types and the juxtaposition of habitat patches to one another is what is important, not the time spent in each habitat type. Similarly, deer and elk often seek shelter in forests and forage in edge or open areas. The time spent in each habitat is irrelevant to the importance of each. Habitat "preference" for snowshoe hares is determined by predator pressure, not optimal food conditions; distribution of moose, *Alces alces*, may be limited by interspecific interactions with white-tailed deer, *Odocoileus virginianus*; and habitat use by red-winged blackbirds, *Agelaius phoeniceus*, varies depending on the presence or absence of yellow-headed blackbirds, *Xanthocephalus xanthocephalus*. Habitat preference is often used as a mathematical and not a biological measure of importance or preference (Porter and Church 1987).

6. Species habitat association studies do not take advantage of the scientific method for conducting research. The scientific method has six parts; (1) make an observation (or documentation from the literature), (2) list *all* reasonable alternative hypotheses that could explain this observation, (3) design an experiment (observational or manipulative) that allows for rejection of each hypothesis independently, (4) conduct the experiment (or gather the data), (5) analyze data, and (6) draw conclusions. The species-habitat association studies do not test hypotheses. More importantly they are not designed to reject alternative hypotheses. Species-habitat association studies use a reductionist approach to look for positive correlations with one or a few habitat features and do not address alternative explanations for the observation. Research projects that have *a priori* hypotheses that are rejectable with the data gathered in the study make a greater contribution to science than do correlational studies that do not provide a basis to reject alternatives.

7. Species-habitat association studies ask the wrong question. These studies are descriptive and address the "what," or proximate mechanisms questions rather than "why" or ultimate causes questions (Gavin 1991). The question should be not only "what," but "why" certain factors determine the distribution of a given species (or more importantly, determine survival and reproductive success). The requirements for life for any species include physiological adaptations to the abiotic environment, ecological adaptations to the biotic environment, and behavioral adaptations to the social environment. Therefore the questions are, (1) is the species physiologically adapted for a given habitat (environment), (2) can it find enough food on which to live, (3) can it survive (avoid predators

and competitors), and (4) can it find a mate and nest site and breed successfully? Once these questions are answered, the conclusions have direct application to management or any other scientific objective. The correlation of a few individuals in a subpopulation in a small portion of the species" total range to a few habitat structural features might prove quite insignificant and irrelevant once these four questions are answered.

8. Correlational studies cannot demonstrate cause and effect. In the case of habitat features, these measurements supposedly indirectly measure predator avoidance and access to food and shelter, though this is rarely demonstrated (but see references in Verner *et al.* 1986). A real danger exists in making use of indirect measures where results can often be misleading. For instance, take an analogous situation. If I were to place radiotransmitters on 30 biologists and follow them around for three months, I might conclude that their use of habitats includes 30% time in brick buildings, 30% in wooden buildings, 20% outdoors, 10% in motor vehicles, and 10% other. This tells me nothing at all about where the biologists find food (access to resources), avoid predators or competitors (seek shelter), or seek mates and rear offspring (maximize their fitness). If the grocery store moved from a brick to a steel building or a biologist transferred from an indoor administrative position to an outdoor field laboratory, the results would be invalidated. Whereas, if my objectives were to predict that the 30 biologists will occur where they have access to resources (food and shelter = employment) and mates, I would have direct measurements of individual needs and results that were predictive. If I could measure reproductive success of each individual and correlate it with the habitat variables measured, I would have the ultimate measure of the importance of the different variables. If I wanted to ask where a species *could* live, I would be better off measuring a food source, shelter, and presence of predators or competitors, than I would measuring diameters of trees or percent ground cover of moss or logs. These latter measurements are only valuable if I have statistical confidence in how they relate to the former factors through time and space.

9. Habitat-association studies focus on a species' ecological surroundings and do not consider the evolutionary or behavioral aspects of why animals do what they do (Gavin 1991). A sound theoretical base is available for asking questions based on the functional significance of space use. For instance, theories on aggression and territorial defense, mate selection, parental strategies, and optimal foraging behavior predict that home range size, shape, and defense should shift seasonally with respect to availability of different food resources, access to mates, protection of young from infanticide, and vulnerability to predators (Krebs and Davies 1993). Questions asked in species-habitat association studies are about the species, whereas selection for these traits acts on individuals and not species or even subpopulations. Also, an application of evolutionarily stable strategy theory (Maynard Smith 1982) to habitat or nest site selection would place the results within the framework of natural selection.

10. Wildlife habitat-association studies do not measure fitness. Darwin's theory of evolution by natural selection is the central and unifying paradigm for all the life sciences. The only true measure that is relevant in any ecological study on a species is fitness, one that is overlooked in habitat-association studies. Although this measurement is difficult to get, it is not impossible and should be attempted whenever possible. Whether a species exists in old growth forests, pole size-class timber, north- or south-facing slopes, or coniferous or deciduous forests, if individuals are surviving and reproducing at the same rate as in "preferred" habitat, then any habitat-association measure is superfluous. Species are often much more resilient and adaptable than can be interpreted from a few habitat measurements. I do not doubt that most, if not all, species could expand their range and use more of existing habitats if they were not disturbed or preyed upon by humans. Therefore, some measure of human activity or disturbance is probably much more meaningful than is some measure of habitat variables.

I strongly encourage vertebrate biologists to consider "what is the question" before they embark on a detailed methodology that has limited application to the endpoint desired. Researchers must define the goal of a species-habitat association study. Is it to predict occurrence? to choose "best" habitats for preservation or management? to provide baseline data to manipulate or create wildlife habitat? to describe patterns or explain processes? or what? A good clear objective, set of testable hypotheses, and appropriate methodology will lend predictability and applicability to the

results. In that the future of many wild populations is in jeopardy, precise and conclusive research on wildlife habitat is essential for continued preservation of threatened species and ecosystems. Perhaps measures of the functional relationship of biotic, abiotic, and social environments will provide a sound basis for accomplishing these goals. I hope this comment will be seen in light of contributing to this goal.

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