DENSITY AS A MISLEADING INDICATOR OF HABITAT QUALITY

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Abstract: Current methods of evaluating wildlife habitat for management purposes can be arranged in a hierarchy of increasing generality. The most general level is evaluation of wildlife habitat for entire communities on the basis of inferences drawn from vegetational structure. At the base of the hierarchy the high resolution studies, upon which accuracy at the higher hierarchical levels depends, usually assume that habitat quality for a species is positively correlated with the density of the species. If habitat quality for a wildlife species is a measure of the importance of habitat type in maintaining a particular species, habitat quality should be defined in terms of the survival and production characteristics, as well as the density, of the species occupying that habitat. Situations in which habitat quality thus defined is not expected to be positively correlated with density are described, along with the species and environmental characteristics that are most likely to produce these situations. Examples drawn from the literature in which density and habitat quality are not positively correlated are described. The positive correlation of density with habitat quality in specific instances cannot be assumed without supporting demographic data.

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The foundation of any wildlife habitat management plan is the ability to assess habitat quality accurately. Without this key ingredient, the effort put into carefully prepared objectives and elegant categorizations of habitat types is largely wasted. Yet biologists often dwell on objectives and categories while treating lightly the assumptions implicit in their assessments of habitat quality. For instance, they seldom question the assumption that the density of a species in a habitat is a direct measure of the quality of that habitat. Perhaps this is because any more accurate investigation of habitat quality to truly reflect the importance of that habitat in maintaining wildlife species populations must be intensive, often at the expense of the broader information base that could be achieved by simple surveys. Such surveys are a particularly common means of evaluating nongame wildlife habitat.

The objectives of this paper are to provide some examples of situations in which this correlation does not hold, and to make predictions regarding species and environmental types for which the density–habitat quality relationship is likely to be decoupled. In such cases, management policies based directly on species abundance may be misleading and these errors may be amplified when management approaches are restricted to the higher levels of the hierarchy.

This paper is dedicated to the late O. C. Wallmo, who was always eager to discuss ideas and whose refusal to be anything but completely honest in evaluating his own ideas, objectives, and research ideas, as well as those of others, set an example for us to follow.

METHODS OF HABITAT EVALUATION

Habitat assessment procedures can be visualized in a 3-level hierarchy of increasing generality in which the accuracy of predictions at 1 level is dependent on accuracy at the next lower level (Fig. 1). The lowest level is the assessment of the habitat relationships of individual species at a particular site. Accuracy at this level is dependent upon an intimate understanding of the demography of the species and of the factors influencing population levels through their influences on survival and production, although such analyses are often abandoned in favor of simple estimation of total density. Biases of the different censusing techniques are a problem, particularly when these are habitat dependent, as are many of the bird censusing techniques (Emlen 1971) and most mammal censusing techniques where home range size varies among habitats. At the next higher level, the species–habitat relationships are extrapolated to sites not actually sampled. The success of this inference is dependent upon the correct identification of the important factors influencing density in the higher resolution studies. At the highest levels of the hierarchy, the extrapolated information is used to put together a habitat quality assessment for an entire wildlife community. Generally, in evaluating the effects of management options on the wildlife community, species interrelationships such as competition and predation are ignored and the community assessment is based solely on the aggregation of individual species assessments.

Over the last decade there has been considerable pressure to develop rapid means of habitat-quality assessment, such that the higher-resolution levels at the base of the hierarchy (Fig. 1, levels 1 and 2) are skipped altogether. For instance, in 1 approach maximizing species diversity is assumed to be the primary objective of management and this diversity is assumed to be directly correlated with habitat diversity (Asherin et al. 1979). There are several problems associated with this approach. First, maximum diversity achieved in the limited areas being managed (α diversity) may not produce maximum diversity on a larger scale (β diversity) (Samson and Knopf 1982), because some wildlife species, such as old-growth specialists, are not adapted to areas of high habitat diversity. Maximizing plant community diversity on a local scale selects for the generalist wildlife species common to disturbed habitats and may ignore the sensitive species with greater habitat specificity. Second, habitat diversity and wildlife species diversity are not always positively correlated; this depends on the ratio of generalist to specialist wildlife species in the area being managed and the specific requirements of those species.

Assessment of a range of habitat types for the presence or absence of wildlife species is a procedure at the 2nd level of resolution. The general objective in this case is to manage lands so that sufficient habitat types are retained to allow for representation of all species while maximizing diversity within this constraint (Thomas 1979). Determination of the presence or absence of species is usually based on the available literature; there is no explicit treatment of the densities required to avoid extinction (minimum viable populations) or of home range size and no evaluation of habitats on the basis

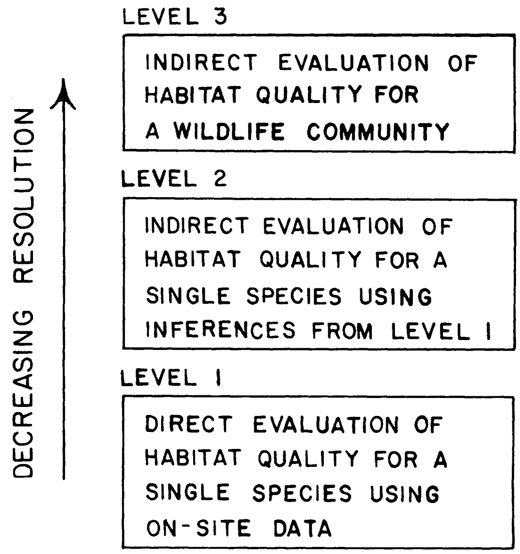

Fig. 1. Hierarchical description of habitat quality assessments.

of wildlife species densities or the relative favorability of the occupied habitats.

Another example of a procedure at this 2nd level of resolution is the U.S. Fish and Wildlife Service's Habitat Evaluation Procedures (HEP) (Flood et al. 1977). This procedure relies on assessment of habitat requirements of individual species taken from the literature, followed by assessment of habitat types based on the ability of each type to provide for these requirements. The 2 major problems with this approach are that our knowledge of species requirements is often poor and synergistic effects among resources are ignored. Thus, a habitat that provided cover but no food would still get a positive value rating, even though the species might not be able to exist in that habitat. Likewise, the sum of 2 "good" resource attributes might well be greater than their separate values.

All 3 of the above methods allow for rapid habitat assessment without direct censusing of wildlife species. They are thus based on untested inferences about which species "ought" to occur in each habitat type and are not suited to management for viable population levels.

ASSUMPTIONS OF HABITAT EVALUATION

The assessment of individual species–habitat relationships is the lowest level of the hierarchy; these data are critical to the success of the HEP type of analyses. The usual assumption at this level is that the local density of a species is positively correlated with habitat quality. Often a range of habitat variables is measured and correlated with species density. Multivariate procedures are used to reduce the number of variables and to aid in interpretation of results (e.g., Carey 1980, Maurer et al. 1980). Although this type of habitat assessment depends more explicitly on density as an indicator of habitat quality than do assessments at higher levels of generality, it has been suggested that the accuracy of any habitat rating technique, such as HEP, should be tested by comparing habitat ratings to the observed relative abundances of a variety of wildlife species (Whelan et al. 1979).

Thus, the assumed positive correlation of a species' abundance with habitat quality underlies most methods used for assessing habitat quality and is explicit for the species-specific level of resolution. It is therefore the basis for a broad range of management decisions regarding wildlife communities.

The assumed relationship often breaks down under intensive study. One reason that it may break down, particularly in northern climates, is that habitat use in winter is critical, whereas most censuses and surveys are taken in warmer months. For northern deer (*Odocoileus* spp.), the availability of winter range may contribute disproportionately to carrying capacity (and thus survival and reproductive patterns) (Wallmo et al. 1977). Identification of habitat quality on the basis of summer densities would thus be misleading; retention of the summer habitat type would not serve to maintain the population if the winter range was destroyed.

A 2nd reason for a breakdown in the density–habitat quality assumption is that there may be multi-annual variability in local population densities that reflects small-scale variability in the food source, in predator populations, or in abiotic environmental factors. Densities may thus reflect conditions in the recent past or temporary present, rather than long-term habitat quality. For instance, site tenacity in breeding passerines can produce local densities that reflect past, rather than current, habitat quality (e.g., Hildén 1965, Rotenberry and Wiens 1978).

Third, social interactions may prevent subdominant animals from entering what is actually the high-quality habitat, while at the same time suppressing reproduction in the high-quality habitat. The surplus individuals may then collect in habitat "sinks," where densities may fluctuate widely (Lidicker 1975). Animals in the low quality sinks survive and/or reproduce poorly. Thus, in a good year, the source population may produce a large excess of juveniles that will emigrate and build up to high densities in the sinks. Because the juveniles are subdominant, there is no social interaction factor to prevent high densities in the sink habitats, which is in contrast to the adult-dominated high-quality or source habitats. Densities in the lower-quality habitat may thus actually be greater at times than in the high-quality habitat. A similar scenario is embodied in the theoretical model of habitat occupancy developed by Fretwell and Lucas (1969). In this model, the movement of individuals into poor habitat is a reflection of individual fitness maximization. According to the model, the per-individual probability of success for unestablished immigrants may be higher in low-quality than in high-quality habitat, because high densities in the high-quality habitat promote a high probability of failure to reproduce successfully and a high mortality rate among the unestablished immigrants. Thus, it may be individually advantageous for them to settle in the lower-quality habitat.

DEFINITION OF HABITAT QUALITY

Fitness of an individual animal (Fisher 1930) is a relative measure that increases with increasing survival probability and increasing offspring production. I propose that habitat quality be defined as the product of density, mean individual survival probability, and mean expectation of future offspring, for residents in 1 area as compared to other areas. More precisely,

$$Q_j = \frac{\left\{\left[\sum_{x_j} n_{x_j}(l_{\alpha_j}B_{x_j} + P_{x_j})\right] \Big/ \sum_{x_j} n_{x_j}\right\}(1/a_j)}{\sum_i \left\langle\left\{\left[\sum_{x_i} n_{x_j}(l_{\alpha_i}B_{x_i} + P_{x_i})\right] \Big/ \sum_{x_i} n_{x_i}\right\}(1/a_i)\right\rangle} \quad (1)$$

where Q_j is the relative quality of habitat j for the species, B_x is the fecundity of an x-year-old and l_α the probability that the offspring will survive to α, the 1st age of breeding. P_x is the probability of surviving from age x to age $x + 1$, n is the number of individuals in each of the i habitats being compared, and a is the area that includes all sampled individuals in the ith habitat. The areas must encompass the home ranges of the individuals included. Conceptually, this is a measure of mean individual "fitness" per unit area. "Fitness" is used here in a management rather than an evolutionary context; it describes a mean group characteristic in 1 habitat as compared to other habitats, rather than comparing 1 individual of a population to other individuals of the population. The measure of habitat quality thus has components of density, offspring production, and survival. High density alone does not infer quality habitat. To give an extreme example, one could imagine a habitat in which all animals were immigrants and none emigrated or reproduced. The quality of the habitat would be zero. If either individual survival probability or number

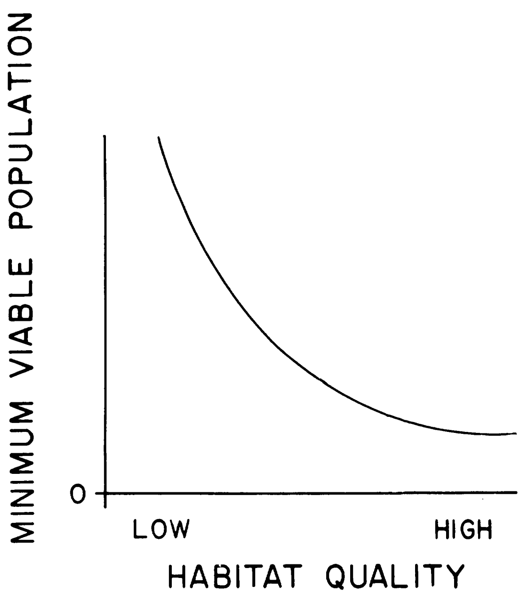

Fig. 2. Change in minimum viable population size with increasing habitat quality.

of offspring produced is zero, then the habitat is making no contribution toward maintaining populations of the species and its quality is zero.

Given this definition of habitat quality, the minimum viable population size will be greater in low-quality than in high-quality habitat, because low survival and production rates in low-quality habitat mean that a higher density is needed to ensure persistence of the species in that habitat (Fig. 2).

To measure habitat quality, one must determine the mean production and survival characteristics of each age-class and the number of resident individuals in each age-class in each habitat. Such a determination will be impractical for most studies. The above formula is thus presented to clarify the definition of habitat quality and provide an ideal standard. This measure of habitat quality may be approximated sufficiently through intensive demographic study of single species in a variety of habitats. In this way one can separate low-quality habitats, which may contain largely immigrants that are unlikely to survive or reproduce well, from higher-quality habitats, containing a lower density of animals but in which densities are more stable, reproductive output of the population is dependable, and the population is more likely to persist in poor or "crunch" years. Where such intensive demographic study is impractical, density-based estimates could be greatly improved through attention to immigration patterns, to adult survival, and to the production of juveniles that survive to reproduce.

The actual parameters used in equation 1 will be means for a certain time period, commonly a year. An accurate assessment of habitat quality requires the calculation of a grand mean and variance over several such time periods. The number of time periods required for a useful measure of habitat quality will be greater for highly unpredictable habitats.

There are some problems inherent in the use of this habitat quality measure. The areas encompassed by habitat patches a_i may in some cases influence survival and production characteristics, particularly for wide-ranging species. This will result in lower Q_j's for smaller patches containing habitat equivalent in quality to that of the larger patches. Area of the patches considered is thus an implicit variable influencing Q_j. Calculating Q_j's for large or for similar-sized patches will remove the area effect. Calculating Q_j's for different-sized patches with similar habitat characteristics will make the area effect explicit. Also, home ranges may encompass several patches of what we perceive as different habitat types, and the delineation of areas for which favorability is to be determined must thus be somewhat arbitrary. Further, the patches used by a species may be from widely separated areas, as for migratory birds. In such cases, it may be useful to make separate assessments of summer and winter range, and of the degree to which different habitat types in each of these ranges contribute to mean relative fitness.

I have defined habitat quality in terms of a single species. The habitat quality for a wildlife community is the sum of habitat qualities for species members, as modified by the effects of species interaction. I have discussed the problems of simply equating habitat quality with diversity. Although it has been asserted (Cringan et al. 1979) that more community-level research is needed as input to the development of habitat management plans, a valid assessment of the effects of habitat manipulation at the community level is dependent upon the accuracy of assessments at the individual species level. In most cases, our understanding of individual species–habitat relationships is still rudimentary.

EXAMPLES

Several examples of situations can be considered in which habitat quality and species density are not positively correlated, because of the influence of social dominance factors. In my own studies of a series of populations of *Peromyscus maniculatus* in spruce (*Picea* spp.) and hemlock (*Tsuga* spp.) stands of different seral stages in southeast Alaska (Van Horne 1982), the populations occurred at a high latitude (55°N) where there was no breeding by young of the year and the dominant adults were clearly separable from the subdominant juveniles on the basis of weight, pelage, and trapping history. Because of forced emigration, reproductive success in different habitats was difficult to estimate. Overwinter survival, however, was a critical component of fitness because there was no breeding by young of the year.

Two different habitat types were distinguished for both adults and juveniles by discriminant function analysis: those characterized by high densities or low densities of the age-class. Individual animals whose home ranges encompassed high-density adult habitat had a significantly higher probability of surviving over the winter period than those whose home ranges encompassed low-density adult habitat, whether these animals were adults or juveniles. Thus, high-quality habitat could be distinguished by the adult habitat discriminant function and appeared to be positively correlated with overwinter survival for both age-groups. The opposite was true of the juvenile discriminant function, for which the habitat characterized by high densities of juveniles conferred lower overwinter survival probability. Thus, high-density adult habitat was of high quality, while high-density juvenile habitat was of low quality.

These quality inferences were corroborated by the observation that adult male weights on the grid containing mostly high-density adult habitat were significantly higher than those on the other trapping grids and the population density on this grid was relatively stable. However, in 1979, the last year of the study, total densities on those grids containing mostly low-quality habitat exceeded those on the grid containing mostly high-quality habitat. This was due to irruptions of juveniles that consisted largely of immigrants that were probably forced into the lower-quality habitat. Additional evidence for the importance of intraspecific dominance interactions in these populations came from breeding inhibition in high-density populations and from the observation that subdominant juvenile diets were of lower quality when these animals were found in high-density populations. Thus, the densities measured in 1979 would have been a completely misleading indicator of overall habitat quality.

Other studies of small mammal populations have reported similar patterns. Kock et al. (1969), for example, found the highest densities of lemmings (*Lemmus lemmus*) during a population "peak" farthest from the optimum habitat as defined by food availability. Animals in the lower-quality habitat tended to be smaller and were probably younger subdominants.

States (1976) reported that subdominant yellow-pine chipmunks (*Tamias amoenus*) accumulated in marginal habitat where their survival probability was relatively low. A large component of these marginal populations consisted of immigrants. Thus, the marginal areas appeared to be acting as dispersal sinks for animals forced out of the central areas, and density in the range of habitats investigated was not correlated with habitat quality.

In an in-depth radio-tracking study, Schantz (1981) found similar numbers of red foxes (*Vulpes vulpes*) in mineral soil and peat soil habitats. He was able to identify the mineral soil habitat as being of higher quality despite the similarity in density, as it contained a higher proportion of reproducing adults.

Similar observations have been made for breeding passerines. Fretwell (1969) reported that there was "no positive correlation between density and suitability" for breeding field sparrows (*Spizella pusilla*) where suitability was measured in terms of breeding success; densities were higher in an area where breeding success was lower. O'Connor (1981) summarized data for a number of migrant and non-migrant bird species in Great Britain. The species showed a pattern of filling only a certain, presumably preferred, habitat when densities were low, but filled the less preferred habitats when densities were high. These species included the wren (*Troglodytes troglodytes*), the chiffchaff (*Phylloscopus collybita*), the great tit (*Parus major*), the yellowhammer (*Emberiza citrinella*), and the Eurasian kestrel (*Falco tinnunculus*). For these species, density would be a reasonably good measure of habitat quality in years of low-overall density, but would be a misleading indicator in years of high-overall density.

When breeding birds are territorial and favorable habitat is limited, a surplus of adults of breeding age ("floaters") may accumulate in poor habitat where either no breeding takes place or where breeding attempts are largely unsuccessful. Thus, a group with low current "fitness" may be found in moderate densities in poor habitat. This phenomenon has been reported for great tits (Krebs 1971), the Santa Cruz Island scrub jay (*Aphelocoma coerulescens*) (Atwood 1980), and the Australian magpie (*Gymnorhina tibecen*) (Carrick 1963).

PREDICTIONS

Problems with assuming density to be a measure of habitat quality are thus found over a wide range of taxa. We are left with several important questions. To what extent can we extrapolate these findings to other species? How general is this lack of close relationship of density to habitat quality? Where do we expect to find density and habitat quality to be decoupled? I suggest that this phenomenon might be found in association with 3 main environmental types (Table 1). The 1st is highly seasonal habitat in which different habitat types may be preferred at different seasons, such that the density–habitat quality relationship cannot be inferred from surveys or censuses taken during only 1 season. The real high-quality habitat in this situation would be that which in some way

Table 1. Factors that increase the probability that density will not be positively correlated with habitat quality.

Environmental characteristics	Species characteristics
Seasonal habitat	Social dominance interactions
Temporal unpredictability	High reproductive capacity
Patchiness	Generalist

was most critical for successful individual survival and reproduction. A 2nd environmental attribute is unpredictability over time. This would allow for opportunistic density increases in low-quality habitat, or overflow into lower-quality habitats during periods of high production and high overall density. Third, habitat must be patchy on a scale allowing for migration between patches if environmental unpredictability is to produce wide density changes in the resident animals of 1 habitat type relative to other habitat types. High densities in low-quality habitat could not be observed if there was no source pool in nearby high-quality habitat.

I would predict 3 main species characteristics to be associated with the habitat quality–density decoupling (Table 1). First, the species should have a social pattern of dominance interactions where it is found in stable populations in high-quality habitat. This type of dominance social interaction is common to a wide range of vertebrates. Its demographic effects are most pronounced in those animals with a 2nd species attribute, high reproductive capacity. This high reproductive capacity can allow "sink" populations to reach high densities when the environment becomes temporarily favorable. Third, this decoupling should be most characteristic of habitat generalists. This is particularly important as such generalists may be used as indicators of habitat quality for a variety of species in those cases where habitat-quality ratings are based on actual survey or census data. This is because generalists are relatively easy to survey and are more likely than specialists not only to occupy a wide range of habitats, but to be found in high densities in at least some habitat types and to have a high reproductive capacity. The 3 species characteristics are more closely associated with small, than with large, body size.

It is likely that for rare species, density may remain a reasonably good indicator of habitat quality if seasonal changes in habitat use are taken into account and if habitat is not patchy. If the habitat is patchy, the presence of a rare species in a given patch will have a larger stochastic element than the presence of a common species in a habitat patch, because of the susceptibility of rare species to local extinctions (e.g., Hanski 1982).

MANAGEMENT IMPLICATIONS

Management plans that depend only on habitat characteristics to infer habitat quality contain a large amount of guesswork, both with regard to viable population levels and with regard to predicatability of species densities on the basis of habitat characteristics. Such plans depend heavily on the correct identification of favorable habitat for the wildlife species being managed. Intensive multi-annual demographic study of a single species over the range of habitats being measured is needed to interpret the broader surveys. Without attention to demography, even multi-annual surveys or censuses will not necessarily be sufficient to distinguish "source" and "sink" habitats. Management plans adopted on the basis of a species survey or census taken during only 1 year, or on the basis of measured habitat characteristics coupled with inadequate knowledge of the factors actually determining habitat quality, are particularly unsatisfactory.

Thus, we cannot afford to ignore the processes that produce the densities we observe, or attempts to maintain target densities by retaining areas of specified habitat types will founder. We need to be much more careful in identifying high-quality or critical habitat and not assume simple density–habitat quality relationships without the demographic data to support them.

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