USABLE SPACE: THE FOUNDATION FOR QUAIL MANAGEMENT

FRED S. GUTHERY, Department of Forestry, 008C Agriculture Hall, Oklahoma State University, Stillwater, OK 74078, USA

Abstract: Two philosophies of habitat management for northern bobwhites (*Colinus virginianus*) prevail nowadays. The quality continuum hypothesis states that quail abundance increases with habitat quality, as governed by food supplies, diversity of plants and animals, and interspersion of habitat types. The usable space hypothesis states that variation in habitat quality, as defined, does not affect quail abundance, and that abundance varies with the amount of space that is usable through time. Supplemental feeding, food plots, supplemental watering, and the creation of additional edge have been demonstrated to be neutral management practices in field experiments. Conversely, creation of additional space to live has been associated with increased abundance in field experiments. At this time, the proper management philosophy seems to be to create additional space for coveys to occupy. If all space on a management area is usable all of the time, nothing further can be done for bobwhites in the name of habitat management.

Introduction

The most obvious philosophy for managing quail habitat is that habitat quality exists, and it is the manager's job to improve the quality of habitat on an area. Habitat quality is a nebulous concept. Generally, quality is thought to vary with food supplies, diversity of plants and animals, and interspersion of habitat types. Under the quality continuum hypothesis (Taylor et al. 1999), it is assumed that the abundance of game birds increases as habitat quality increases.

A less obvious philosophy for managing habitat is that habitat is either usable or not usable, and that quality as defined above is a secondary if not minor management concern (Guthery 1997). Under this philosophy areas (as opposed to habitat) have quality, which is defined as the proportion of space that is usable. However, any block of habitat on an area is either usable (quality = 1) or not usable (quality = 0). If space is usable, its quality cannot be improved, but it can be degraded to where it is not usable. Taylor et al. (1999) termed this outlook the binary quality hypothesis, but I prefer to call it the usable space hypothesis.

Under the continuum hypothesis, management focuses on increasing food supplies, diversity, and interspersion of habitat types. Under the usable hypothesis, management focuses on recognizing and rehabilitating space that is not usable. Managers remodel quail houses under the continuum hypothesis and build new ones under the usable space hypothesis.

I developed the usable space hypothesis in the 1990s (Guthery 1997). I sought an omnibus explanation for variation in bobwhite abundance among areas. I had been on scores of ranches providing technical guidance on management. I was also familiar with the research literature on bobwhites and other quails from throughout North America. This experience and reading, plus a good deal of thinking, led me to the realization that, although areas with high quail populations differ in habitat structure and composition, there is a common theme on all such areas. The areas are saturated with usable space that is available all the time.

My purpose is to compare and contrast the quality continuum and usable space hypotheses. I will discuss the history of the usable space hypothesis, explain how usable space governs quail abundance on areas, review the theoretical and practical support for the usable space hypothesis versus the quality continuum hypothesis (hereafter, continuum hypothesis), and discuss shortcomings of the usable space hypothesis (hereafter, space hypothesis).

History

The space hypothesis has been around, in one form or another, since the 1930s. I want to directly quote the writings of some of the pioneers in game management:

"[D]evelopment of all types of quail preserves ... consists in diversifying the vegetation as much as possible and providing a balance of open woodlands, weedy fields, cultivated and fallow ground, thickets, and scattered grass ... areas of proper density and small extent, for this is the most favorable environment for bobwhites. It provides the essentials in each range and the maximum number of covey ranges."--Stoddard (1931:374)

Stoddard mixed elements of the continuum and space hypotheses. Interspersion, diversity, and foods ("weedy fields") fit the continuum hypothesis. Note the last sentence, however, which relates to the "maximum number of covey ranges." This is the essence of the space hypothesis.

"The highest quail populations recollected by old-timers on their home farms in the early days of settlement fail to show any *former* populations in excess of a bird per acre. This indication, if substantiated by fuller data, means that the period of great abundance in quail ... consisted of a *higher proportion of populated acres*, rather than a higher maximum population per acre than now obtains."--Leopold (1933:52)

Leopold is saying quite simply that in the heyday of bobwhite abundance in the Midwest, there were more quail because there was more space for them to live in, not because density (habitat quality) was higher where they lived. I want to point out that we have densities today (late Twentieth Century) as high as any ever recorded.

"Experience on game management areas has shown that efforts to raise carrying capacity are more likely to be fruitful if emphasis is placed upon the creation of new covey territories...."--Errington and Hamerstrom (1936).

This statement sums up the space hypothesis pretty well, except that it makes no mention of time.

"To supply most of the needs of high populations of quail, they must be assured continuous use of virtually every square foot of ground."--Lehmann (1984:189).

Lehmann (1984) invoked the time issue. His words capture the essence of the space hypothesis.

When I was developing my version of the space hypothesis, I was not aware of the thinking that preceded mine. The human condition insures that we often do not perceive concepts until we are willing to perceive them. Accordingly, I, like most wildlife biologists, was ensnared by the continuum hypothesis. My role in development of the space hypothesis was seeing its power, owing in large part to the clarity research results have added to our understanding of quail populations over the past several decades. The early workers were not privy to these results.

Description and Definitions

The space hypothesis states that the average abundance of bobwhites on an area is proportional to the quantity of habitat space-time available on the area. Space-time is the product of space and time. For example, if 100 ha (250 acres) were usable for 365 days a year, the quantity of space-time would be 36,500 ha-days (91,250 acre-days). Space-time is a convenient way of invoking Lehmann's (1984:189) recognition of the opportunity for "continuous use of every ... square foot." Usable space may be considered a small area (patch) of habitat to which bobwhites respond in a use or no use manner. A management area may be considered a collection of such patches. Usable space is compatible with the physical, physiological, and behavioral adaptations of bobwhites. Habitat in usable space must be of the proper structure to fit physical and behavioral adaptations; it must not be too hot or too cold to fit physiological adaptations.

Theoretical and Practical Support for the Space Hypothesis

Biologists have a penchant for discussing the fitness of native animals. Fitness is a conglomeration of survival and reproduction that leads to declining, stable, or expanding populations. Taylor et al. (1999) pointed out that a condition of the continuum hypothesis was that fitness varies with habitat quality; populations expand and densities increase as quality (through its effects of fitness) goes up. They mistakenly argued that the space hypothesis is founded on constant fitness, which cannot exist or we would have no variation amongst individuals. However, the space hypothesis does require that the average fitness in populations converges to similar values, given frequency and severity of weather catastrophes. This convergence seems to be well demonstrated in bobwhites populations. Populations differ among latitudes because of exposure to different types of weather catastrophes (Guthery 1997, 1999*b*).

There are 2 ways to interpret convergence in fitness. Either habitat quality is the same everywhere or usable space is the same everywhere. If habitat quality is defined according to food supplies, diversity, and interspersion, then it cannot be the same everywhere because these variables differ from site to site, area to area, and region to region. If habitat quality varies and fitness remains the same, given latitudinal effects associated with weather catastrophes and opportunities to express density dependence (Guthery 1999*b*), where does this leave the continuum hypothesis? It is inconsistent with the nature we observe; it does not work. However, if usable space is usable space, we would expect convergence in fitness and population densities on space that is usable.

Empirical Support for the Space Hypothesis

Another way to compare the continuum and space hypotheses is to determine whether increases in habitat quality, as defined, lead to increases in density. Supplemental feeding and food plots are methods of increasing food supplies and improving habitat quality from this standpoint. Yet, as I pointed out in my formal description of the space hypothesis (Guthery 1997), supplemental feeding is best viewed as a neutral practice--it neither increases nor decreases bobwhite abundance, although it may change the distribution of coveys. Likewise, there is no convincing evidence in the research literature that food plots increase the abundance of bobwhites. The practical results of feeding and food plot experiments accrue in part because the food energy provided by management is trivial relative to the food energy available on farms and ranches (Guthery 1997, 1999*a*). Provision of supplemental water had no effect on bobwhite abundance in South Texas during either rainy or droughty years (Guthery and Koerth 1992).

On the other hand, bobwhite populations increase on areas as usable space is added to an area. The best example comes from Maryland's Eastern Shore (Burger and Linduska 1967). Practices that increased the amount of permanent cover (permanent usable space) increased bobwhite populations, whereas food plots and like practices had no apparent effect. The practices included planting hedges and grasses and reducing grazing pressure. Burger and Linduska (1967) took the bobwhite population on 1,200 ha (3,000 acres) from 5 coveys to 38 coveys in 8 years simply by adding space to live in. They did not practice predator control. Observed Burger and Linduska (1967:1): "Winter cover and nesting cover, not food, apparently were the most important requirements of the quail population."

I managed bobwhite habitat on the Bomar Wildlife Research Area in Duval County, Texas. This provided a personal if nonscientific opportunity for me to test the space hypothesis. When I took control of the Bomar Area, I deactivated all the feeders (1/8 ha, 1/20 acres), shut off the water to the pastures, and quit planting foods. I added 5 clusters of brush shelters to an open pasture, chemically controlled brush, and burned small plots or disced them on about a 2-year rotation to prevent the build-up of herbaceous cover. Such a build-up reduces usable space. In short, the management philosophy on the Bomar Area was to keep all space usable at all times.

The Bomar Area had a higher density of bobwhites than surrounding ranch land for 5 years running. The population fluctuated with rainfall and heat loads, but remained high. One year density exceed 5/ha (2/acre) and the harvest was about 2.5 birds/ha (1/acre). No predator control was practiced, despite the fact that bobcats (*Lynx rufus*), coyotes (*Canis latrans*), and innumerable hawks used the area. For example, when we burned or disced, it was not unusual to have 30-50 hawks concentrate on the area.

Edge, Habitat Quality, and Usable Space

Creation of more edge (higher interspersion) is widely considered to be a method of improving habitat quality. Leopold (1933:132) postulated that potential density of certain types of game, like bobwhites, increases with the amount of edge in the area they occupy. Leopold probably would be embarrassed for professional wildlife management if he knew how his simple, inductive principle has been accepted without challenge, misapplied, and generally abused. Indeed, Leopold would not have formulated the principle of edge as he did if he knew what biology knows now.

Leopold's principle of edge contains a grain of truth. Guthery and Bingham (1992) showed that certain types of edge are associated with increases in the amount of usable space and, when edge increases usable space, the expectation is for abundance to increase, under the space hypothesis.

Guthery and Bingham (1992) also showed that under a large set of circumstances (perhaps most circumstances one would encounter in the field), the creation of additional edge has no effect on the abundance of nondomestic poultry. In other words, on many ranches creation of edge is a neutral management practice, as are food plots, feeders, and supplemental watering. Hanson and Miller (1961) demonstrated the neutrality of edge additions for bobwhites in a field experiment.

Creation of edge fails under many circumstances because the arrangement of habitat patches (woody cover, forbs, grasses) has a property called slack (Guthery 1999*c*). Different arrangements do not affect the amount of usable space and, therefore, do not affect populations under the space hypothesis. Slack arises because bobwhites can alter time in behaviors with null effects on survival and because they are adapted to (fit to live in) a remarkable variety of habitat configurations. Slack also arises because patch types have interchangeable functions. For example, robust herbaceous cover may serve the same purpose as woody cover, and low woody cover may serve the same purpose as herbaceous cover.

Recent research results demonstrate, as Guthery and Bingham (1992) speculated, that too much edge is damaging to populations. For example, the survival rate of ring-necked pheasants (*Phasianus colchicus*) declines with the quantity of edge (Schmitz and Clark 1999). In other words, edge kills. This is not what Leopold (1933:132) had in mind.

Shortcomings of the Space Hypothesis

When I formulated the space hypothesis and developed associated constructs, I worked under the assumption that the quality of a patch could be defined as 0 (not usable) or 1 (usable). This assumption troubled me from the outset and I hedged, pointing out in the appendix of Guthery (1997) that a patch might be more usable than not usable. For example, a patch might be usable to degree 0.9 on a 0-1 scale and not usable to degree 0.1. I also speculated in Guthery (1997) that bobwhite selection for habitat patches with different attributes would show thresholds, or sharp breaks, as determined by the usable-not usable dichotomy.

My subsequent research suggests that neither binary quality nor thresholds in selection fit the habitat use behavior of bobwhites in the field. In collaboration with biologists from Texas, Arizona, and Mexico, I have discovered that habitat patches can be usable to the same degree that they are not usable. In other words, patches with certain properties concerning temperature, brush coverage, bare ground exposure, and exposure to ground and aerial predators may be equally bobwhite habitat and not bobwhite habitat. This is a paradox, like when a glass is at once half empty and half full. However, this same research shows patches can be bobwhite habitat to a high degree or not bobwhite habitat to a high degree (no surprise here, folks). My research team has also found that selection behavior does not exhibit thresholds of preference and avoidance, except possible for temperatures (Kopp et al. 1998). I do not think failure of the binary quality assumption or the threshold prediction seriously impairs the space hypothesis.

What Does It Mean?

The manager can try to improve habitat quality where quail live, or he or she can try to create usable space where they do not live. The quality approach is likely to be neutral or damaging, whereas the space approach is likely to be successful.

A covey of bobwhites probably needs at least 6 ha (15 acres) of space that is saturated with space-time, meaning each and every square foot of space is usable each and every day of the year. The first concern in space usability is woody cover. The J. Grant Huggins 50:50 rule is a good model to follow: "A bobwhite should never be more than 50 yards from a clump of brush 50 feet in diameter." Ground cover between brush clumps should never go below quail height or above 3 times quail height.

When the manager has made all space usable at all times, he or she has done all that is humanly possible to benefit quails in the name of habitat management. Contrary to the continuum hypothesis, the space hypothesis provides an endpoint for management. Populations on areas saturated with space-time will still fluctuate with the weather, but they will maintain high average densities.

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