SLACK IN THE CONFIGURATION OF HABITAT PATCHES FOR NORTHERN BOBWHITES

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Abstract: I analyzed whether reported ranges in the optimal values of habitat features for northern bobwhites (*Colinus virginianus*) reflect incomplete knowledge or a property of the bobwhite–habitat interface. Simple landscape modeling revealed that patch configuration (the dispersion, quantity, and type of habitat patches) has a property defined as slack: different patch configurations with ranges of values for habitat features may provide optimal habitat at the landscape level. Slack arises because different patch configurations lead to fully usable space through time. Slack also may arise because (1) bobwhites are broadly adapted to vegetation structures; (2) the interchange of time allocated to different behaviors has null effects on fitness, within ordinary limits; and (3) patch types have interchangeable functions. Ranges of optimality for habitat features seem to be a property of the bobwhite–habitat interface. Management should address limiting boundary conditions for patch configurations as opposed to seeking a single, population-maximizing configuration. Slack permits flexibility in habitat management plans and thus fosters multiple-use management.

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An ideal landscape for northern bobwhites (hereafter, bobwhite) permits maximum expression of their demographic potential. The search for properties of ideal landscapes has been ongoing since the 1930s. Stoddard's (1931:374) approach to landscape development consisted of "diversifying the vegetation as much as possible and providing a balance of open woodlands, weedy fields, cultivated and fallow ground, thickets, and scattered grass or broomsedge [*Andropogon* spp.] areas of proper density and small extent. . .. [This arrangement] provides the essentials in each range and the maximum number of covey ranges. The greater the number of suitable ranges each with an abundant all-year-round food supply, the more birds the land will [carry]."

Edminster's (1954) model of the ideal landscape (Table 1) was qualitatively similar to that of Stoddard (1931). Edminster added detail on plot size. A property of the Edminster model that has persisted in habitat models is ranges rather than points for descriptions of optimal habitat.

Species–habitat modeling for bobwhites (Schroeder 1985, Bidwell et al. 1991, Rice et al. 1993) is a more recent approach that can be used to identify ideal landscapes. The general process is to develop suitability indices for diagnostic habitat features and to composite the suitability models into a multivariate model (equation) that provides a number (index) presumably correlated with average density of bobwhites on an area of inference. Existing models (Schroeder 1985, Rice et al. 1993) permit a set of habitat features (as opposed to an instance) to reflect optimum habitat at the multivariate level because of ranges in optimal values for single habitat features (Fig. 1). In other words, considering the *n*-dimensional set of habitat features (Hutchinson 1957) to which bobwhites respond, we may find an optimal region based on ranges for diagnostic habitat features as opposed to a single maximizing point based on fixed values of these features.

Ranges of optimality in traditional and current descriptions of the bobwhite–habitat interface may represent empirical uncertainty over what is optimum, or, alternatively, the ranges may reflect a general property of the interface. If the latter holds, then different configurations of habitat patches may result in landscapes of equal and optimal value to bobwhites. This outcome would have important implications for habitat management. Herein, I develop the hypothesis that many different patch configurations may lead to optimal landscapes for bobwhites. I also discuss possible processes underlying this hypothesis, and implications of this hypothesis for approaches to habitat management.

METHODS

Conceptual Background

I assumed bobwhites move through habitat patches in space–time landscapes, integrating

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Table 1. Edminster's (1954) model of an ideal landscape for northern bobwhites.

Cover type	Percentage of total cover	Best unit size (ha)
Grassland	30–40	2.0–4.0
Crop fields	40–60	0.4–2.0
Brushy cover	5–20	0.1–0.4
Woodland	5–40	2.0–4.0

the fitness value of sets of habitat features over some radius of decision that defines patch size. A space–time landscape has 4 dimensions: length, width, height, and time. The radius of decision is defined as the distance over which bobwhites perceive the fitness value of habitat features. Dimensions of the radius are not known, but its existence (or something like it) is known at the patch scale (Kuvlesky 1990). With respect to visibility (screening cover) as gauged by humans, the radius may average 12–13 m, subject to variability (Kopp et al. 1998).

At any instant, a landscape may be considered an infinite set of Cartesian (X-Y) coordinates for a probability surface (Guthery 1997). Associated with each coordinate is a patch with habitat properties. The probability that a point in the landscape is usable is instantaneously either 0 or 1. As time passes, points may be usable for some fraction of elapsed time ranging between 0 and 1 inclusive. Hence, from start to end of a specified period, a probability surface characterizes point usability on a landscape (Fig. 2). The surface defines the probability (proportion of time) that underlying points were usable during the period of interest. Space–time saturation, a realistic goal of habitat management (Guthery 1997), occurs when all points are usable at all times (Fig. 2A). This goal is embodied in the thinking of Stoddard (1931: 374), Leopold (1933:52), and Lehmann (1984: 189). The primary question addressed in this paper is whether space–time saturation may occur under a variety of patch configurations (Fig. 3), which would support ranges of optimality in habitat features. Patch configuration is defined as the dispersion (distribution in space), quantity, and type of habitat patches.

Simulation Experiment

I developed a simple simulation model to explore how space usability varies with the number and size of woody cover objects dispersed within a matrix of herbaceous cover. Known assumptions underlying the model include (1) bobwhite habitat may be characterized based on 2 patch types (woody cover, herbaceous cover); (2) patches of woody cover (hereafter, mottes) were structurally acceptable to bobwhites; and (3) the herbaceous cover was struc-

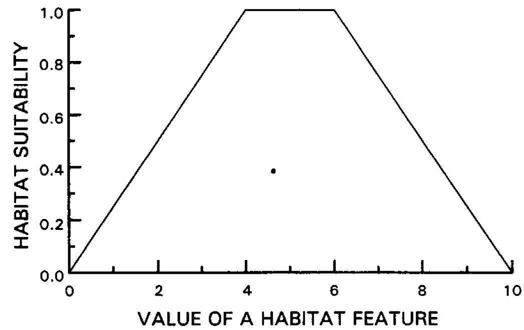

Fig. 1. Typical habitat suitability model for a single habitat feature. The range of X-values where habitat suitability is equal to 1.0 may represent empirical uncertainty or a property of the interface between northern bobwhites and their habitat.

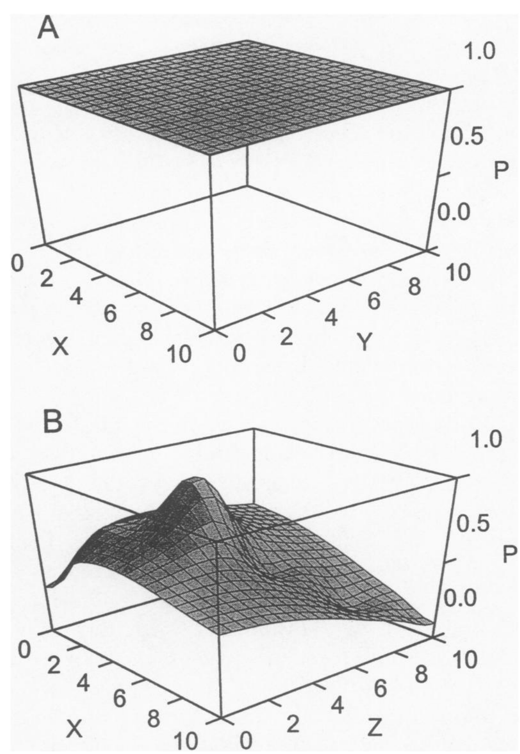

Fig. 2. The conceptual surface giving the probability that a point in a landscape is usable (P) over some period of time; X and Y represent Cartesian coordinates of points on an area. The top figure (A) shows space–time saturation (all points usable at all times), whereas the bottom figure (B) shows a landscape in need of habitat management.

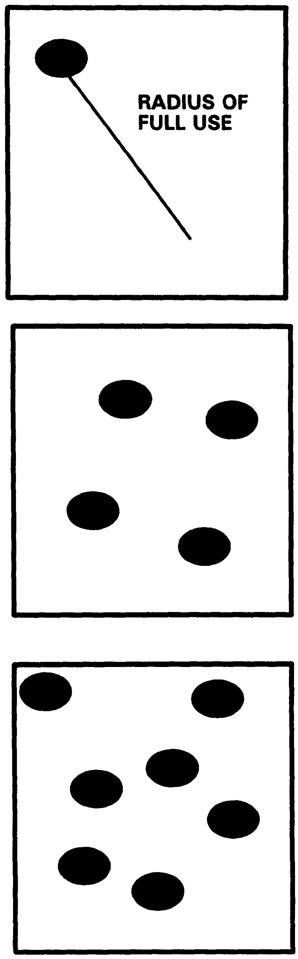

Fig. 3. Schematic diagram of the relation between dispersion of woody cover (circles) in a matrix of herbaceous vegetation and the usability of habitat space by northern bobwhites. (A) Woody cover is deficient, and all points in the square that exceed a distance (the radius of full use) from woody cover are not fully usable. (B and C) These arrangements of woody cover are of equal and optimal value for northern bobwhites because the radii of full use (A) from all woody cover objects encompass all points in the square.

turally acceptable, given the number and size of mottes. The nature of acceptable herbaceous cover varies with the coverage and dispersion of woody cover (Guthery 1986).

The simulation program permitted specification of the number and radius of mottes on a 1-ha area (100 × 100 m). Selection of a square, 1-ha area was arbitrary; however, the simulation results extrapolate directly to areas of any size. Although coordinates for motte centers were chosen randomly, the program forced nonoverlapping canopies, given the specified radius; therefore, placement was not random. The canopy of a motte was permitted to extend beyond the boundaries of the area if the center of the motte fell within the area. For a specified dispersion, density, and size of mottes, the program sampled 10,000 randomly located points and determined the distance to the nearest motte; if a point fell under a motte, this distance was set at 0 m. The minimum distances (n = 10,000) were averaged to obtain a mean minimum distance. Simulations for a specified size and density of mottes were replicated for 5 dispersions, and the mean of mean minimum distances was used in developing a function that described mean minimum distance based on size and number of mottes of fixed size. Dispersion of mottes was variable at constant number and size because locations of mottes were determined stochastically.

I used a concept known as the radius of full use (Guthery and Bingham 1992; Fig. 3) to assess space usability under different motte configurations. Bobwhites are sensitive to distance from woody cover in most environments (Stoddard 1931:181, Lehmann 1946, Murphy and Baskett 1952, Rice et al. 1993). This sensitivity may reflect an evolved sense of security from predation if woody cover is used to escape threats. Security probably declines nonlinearly as distance from woody cover (or an appropriate surrogate such as tall, robust herbaceous cover) increases. The radius of full use is defined as the maximum distance from woody cover where the probability of space use is not conditional on distance. For modeling purposes, a point was defined as usable if it fell within the radius of full use from the edge of a motte or if it fell within the motte; otherwise the point was defined as unusable.

RESULTS

Based on simulation results, the proportion of points usable increased in the form of a confined exponential function of the number of mottes (Fig. 4). Whether an area (1 ha) had 15, 30, 45, or >60 mottes, the proportion of usable space exceeded 0.9 under the constraint established (radius of full use = 25 m). Variability in the relation, illustrated by a jagged rather than smooth line (Fig. 4), occurred because of differences in the dispersion (distribution in space) of mottes.

Another way to analyze space usability relative to number and size of mottes is to consider the mean minimum distance (d) from random

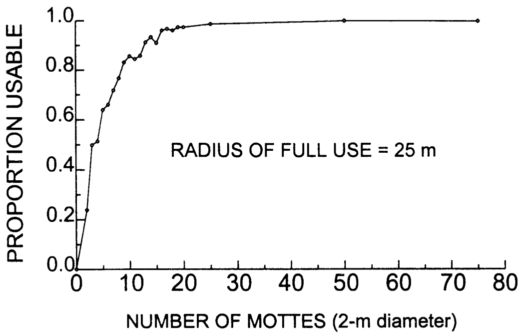

Fig. 4. Simulated relation between the proportion of a 1-ha area (100 × 100 m) usable and the number of 2-m-diameter mottes with the radius of full use set at 25 m.

points to the edge of mottes. The mean is a function of size and number of mottes. The mean declines as a linear function of motte radius for any fixed number of mottes (Fig. 5). The curvilinear plots obscure this outcome because of perspective. Consider a point not in a motte. As the radius of the motte grows, the distance to the edge of the motte declines exactly as the growth distance from some fixed point outside the motte.

At a fixed radius (X) for mottes, the number of mottes predicted mean minimum distance (d) according to

$$d = 58.6N^{-0.5667} - X + 1;\ X, N \geq 1,$$

where N = the number of mottes ($r^2 = 0.99$). The power function would hold approximately if mottes had radii that varied within a narrow (1–3 m) range. The mean minimum distance declines rapidly for any motte size as motte density increases from low (1–2/ha) to moderate (15–20/ha; Fig. 5). As motte density increases from moderate to high (40–50/ha), the mean minimum distance declines slowly. This curvilinear relation shows that the mean minimum distance does not decline in proportion to the number of mottes. For example, increasing the number of mottes from 20 to 50 (150% increase) is associated with a decline in the mean minimum distance from 8.73 to 4.38 m (49.8% decrease). Moreover, 20 mottes/ha would provide about the same sense of security as 50 mottes/ha if the radius of full use was a very conservative distance of 10 m from woody cover. Converting these numbers to approximate canopy coverage (%) of mottes, we could conclude 5.7% canopy coverage is functionally equivalent to 14.1% canopy coverage in terms

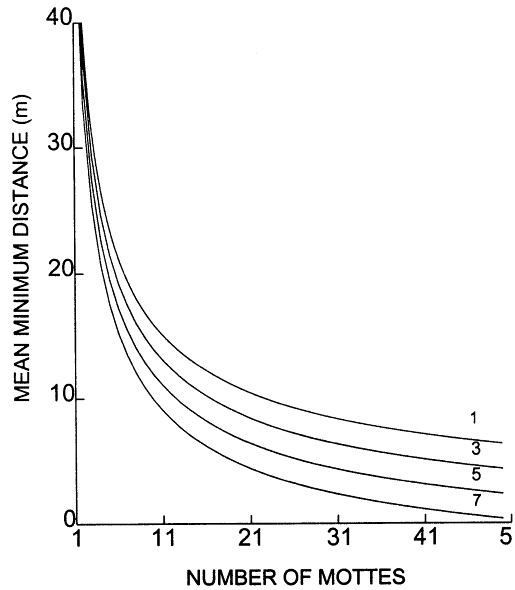

Fig. 5. Functional relation between the mean minimum distance from a random point to a motte and number of mottes per hectare as size of mottes varies. Numbers in the figure give the radii of mottes (m) for the associated curves.

of space usability, if we have 20 or 50 well-dispersed mottes with 3-m radii.

The proportion of space usable varied asymptotically with the radius of full use at different densities of mottes (i.e, the proportion usable approached 1.0 as the radius of full use increased; Fig. 6). The asymptote (1.0) occurred at lower radii of full use as motte density in-

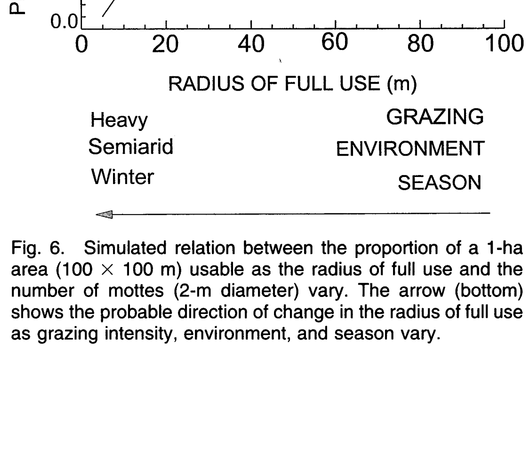

Fig. 6. Simulated relation between the proportion of a 1-ha area (100 × 100 m) usable as the radius of full use and the number of mottes (2-m diameter) vary. The arrow (bottom) shows the probable direction of change in the radius of full use as grazing intensity, environment, and season vary.

creased. Land-use practices or environmental conditions that reduce the radius of full use through effects on herbaceous cover had more marked effects on space usability at lower densities of mottes.

DISCUSSION

The arrangement of patches in a landscape defines the nature of the conceptual probability surface over the landscape (Fig. 2). This statement recapitulates the well-known principle of interspersion (Leopold 1933:132) from a probabilistic perspective: interspersion may be viewed as a set of probability distributions for patch features in a space–time landscape. Based on the simple landscape modeling done above, which demonstrated the potential existence of different patch configurations that lead to fully usable space, optimal landscapes for bobwhites are structurally variable but functionally equivalent. Thus, landscapes seem to have a property I shall define as slack (different patch configurations may lead to fully usable space and, hence, optimal habitat conditions). The existence of slack would mean it is possible to add or subtract patch types and to change their dispersion in space without altering the nature of the probability surface associated with the landscape (Fig. 2).

Slack in patch configurations may arise from ≥3 sources, in addition to that provided by variable configurations under a conceptual construct, the radius of full use. The first source is the remarkable adaptability of bobwhites. Notwithstanding the bobwhite's morphological and behavioral limitations to habitats with certain structures, the suite of suitable structures is vast. One need only consider the geographic range of the species to appreciate its adaptability. The primary range of bobwhites spans latitudes from Guatemala to Michigan, and longitudes from Colorado to Virginia (Johnsgard 1975:82). Flora, fauna, and climate are quite variable within this geographic region.

A second source of slack is interchangeable time. If we consider 2 different arrangements of required patches (i.e., loafing patches interspersed among foraging patches), and if these arrangements have different statistical properties (e.g., mean point-to-loafing-patch distances), then bobwhites may alter time in activities such that each arrangement is equally acceptable. Interchangeable time is that which may be attributed to alternate behaviors with null effects on fitness. Interchangeable time tends to nullify, from a management perspective, variability in distance relations among required patches.

For example, whether a covey spends 10 min under woody cover or 10 min traveling to woody cover makes little difference to the survival of the covey (especially when density-dependence influences fitness). The probability of survival for the 10 min is quite high (near 1.0) under either behavior. Moreover, interchange of time in activities would have minor effects on energy expenditure because thermoregulation, not work as defined in physics, usually consumes most of the energy expended by small birds (Gordon et al. 1968:97), especially in winter (Swanson and Weinacht 1997).

The interchangeability of functions provided by woody and herbaceous cover gives rise to a third source of slack. For example, bobwhites may loaf under taller herbaceous cover or woody cover, forage in herbaceous or woody cover, and so on (Leopold 1933:130; Errington and Hamerstrom 1936:386). This interchangeability permits canopy coverage of woody and herbaceous plants to vary among landscapes while space–time saturation remains constant (i.e., landscapes may be of like quality with variable quantities of patch types).

There likely exists some threshold region where too much woody cover and too little herbaceous cover exists, leading to loss of usable space. If that threshold was breached in the above modeling results, then the arguments on space usability fail.

The present arguments do not preclude the possibility that published ranges of optimality for habitat features for bobwhites represent empirical uncertainty as opposed to a property of the bobwhite–habitat interface. However, the existence of slack in patch configurations seems compelling for evolutionary and logical reasons.

MANAGEMENT IMPLICATIONS

The potential existence of slack in patch configurations puts the practice of habitat management in a different (if not new) perspective. Leopold's (1933) placement of what he called environmental controls (habitat management) as the most recent development in wildlife management theory probably helped generate a tradition among wildlife biologists that habitat management may be taken as, in general, the most rewarding of all management activities for increasing the abundance of wildlife. The tradition undoubtedly is well founded, but managers must recognize that habitat per se, and management thereof, may fail to explain a large portion of the spatiotemporal variation in bobwhite demographics. The slack associated with patch configurations leads to, in theory, situations where habitat management will be nonrewarding if not damaging. Altering patch configuration should have no effect on bobwhite abundance if space–time saturation remains equal before and after management (Guthery 1997). Hanson and Miller (1961) may have been operating in space–time saturated landscapes when they discovered that creation of edge did not influence bobwhite abundance.

In the theory of habitat management for bobwhites and other wildlife species, science may seek to find a single, maximizing set of conditions, if such a set exists. The maximizing set does not seem to exist for bobwhites; rather, bobwhites are well adapted to a virtually infinite variety of patch configurations. The goal of management under this scenario is to recognize boundary conditions (i.e., sets of habitat features or patch configurations where space usability begins to decline). These boundary conditions show where habitat management may be applied with reasonable expectations of a positive population response.

The slack in patch configurations permits flexibility in the application of habitat management practices. For example, the variation associated with management plans, such as the proportion of brush subjected to treatment and the size and dispersion of untreated and treated areas, may have little, if any, differential effect on bobwhite demography if the variation is constrained within certain ranges. This outcome permits altering habitat management plans to accomplish multiple land-use objectives.

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