A PHILOSOPHY OF HABITAT MANAGEMENT FOR NORTHERN BOBWHITES

FRED S. GUTHERY, Caesar Kleberg Wildlife Research Institute, Texas A&M University-Kingsville, Kingsville, TX 78363, USA

Abstract: Northern bobwhites (Colinus virginianus) have received considerable research attention since the 1920s. I evaluated published results for patterns that might be meaningful in developing a general philosophy of habitat management for this species. Bobwhite populations show similar mean demographics (survival, productivity) as climates, landscapes, and predator populations vary about them; this suggests some operational constancy in habitat quality wherever populations persist. Neither food abundance nor habitat type interspersion are satisfactory general predictors of population density on a management area, although interspersion provides a limiting condition (after min. interspersion requirements are met, further interspersion has, at best, neutral effects on density). Long-term, mean density on an area may vary in proportion to the quantity of space (amt permanent cover) that fits the physical, behavioral, and physiological adaptations of bobwhites through time. The goal of habitat management on an area should be to provide bobwhites the opportunity for unconstrained use of space through time (space-time saturation). This common sense outlook seems to have been obscured by unjustified concerns over food and interspersion and lack of a general understanding of successional affiliation.

J. WILDL. MANAGE. 61(2):291–301

Key words: bobwhite, Colinus virginianus, cover, demography, food, habitat ecology, habitat management, habitat quality, interspersion, northern bobwhite.

Few species have received research and management attention equal to that received by northern bobwhites. Natural history research began in the 1920s and resulted in Stoddard's (1931) landmark book. Since then the species' biology, especially foods, ranges and mobility, population dynamics, and habitat requirements, have been thoroughly and repeatedly documented (Scott 1985). Numerous papers have dealt with management practices such as grazing, prescribed burning, food plots, man-made loafing shelters, chemical and mechanical treatments of habitats, food and water supplementation, and combinations of 2 or more of these practices. The time has come to pause and reflect on the knowledge gained from past research and to determine if generalizations can be drawn from the results.

Research results in the bobwhite literature seem to show patterns that are meaningful in developing a general habitat management philosophy. The first is the narrow range of mean demographic variability (survival, production) associated with different climates and landscapes. The second is the usual failure of management practices aimed at improving habitat quality and the consistent success of practices aimed at increasing usable space. A successful practice is defined as one that increases average density on an area. My purposes are to review these patterns, supplement them with theoretical considerations on the role of time in interpreting the bobwhite-habitat interface, develop a conceptual model of bobwhite habitat management, show how to apply the model in management, and provide testable predictions for researchers who want to challenge the model. Finally, I discuss research needs relative to the management model and summarize management implications.

The Caesar Kleberg Foundation for Wildlife Conservation supported this work. I thank the Department of Range and Wildlife Management, Texas Tech University; the Welder Wildlife Foundation; and the Caesar Kleberg Wildlife Research Institute, Texas A&M University-Kingsville. R. L. Bingham, L. A. Brennan, D. L. Drawe, S. P. Glotz, E. C. Hellgren, W. P. Kuvlesky Jr., G. L. McBryde, and J. G. Teer commented on the manuscript.

BOBWHITE DEMOGRAPHY

Time series on the percentage of juveniles in the hunting bag provide data on demographic processes throughout the range of bobwhites in the United States. The percentage of juveniles in the hunting bag has been taken as an estimate of the annual mortality rate. The reasoning is that if populations fluctuate about some average number and show no trend through
time, the increment of juveniles must match the mortality of adults. Differential vulnerability of juveniles and adults to harvest (Shupe et al. 1990, Roseberry and Klimstra 1992) may bias demographic inferences developed from age ratio data, depending on the intensity and duration of hunting (Shupe et al. 1990). Despite possible bias, time series data on age ratios provide a strong index of population processes; we need a method of interpreting the age ratio data in a context meaningful for management theory.

If we eliminate ingress and egress from population processes, we can say next year’s autumn population \( N_{t+1} \) consists of individuals surviving from this year’s autumn population \( N_t \) plus net production by surviving individuals. This statement can be expressed

\[
N_{t+1} = sN_t + sN_tR = sN_t(1 + R)
\]

where

\[
s = \text{annual survival rate}
\]

\[
R = \frac{\text{surviving juveniles per surviving adult}}{}
\]

If populations are stable through time, then \( N_{t+1} = N_t \) and dividing both sides of equation (1) by this constant yields

\[
1 = s(1 + R)
\]

or

\[
s = \frac{1}{1 + R}
\]

and

\[
R = \frac{1}{s} - 1.
\]

Equations (2) and (3) give, respectively, the stabilizing annual survival rate at known production per surviving adult and the stabilizing production per surviving adult at a known annual adult survival rate. For example, bobwhites surviving at an annual rate of 0.053 (Burger et al. 1995) would require productivity of about 18 juveniles per surviving adult for population stability based on equation (3). The graph of either equation (2) or (3) shows all possible simultaneous values for survival and productivity that lead to stability in autumn populations in any 2 consecutive years. Comparison of theoretical and empirical relations based on time series data supports equation 2 (Fig. 1).

Warmer climates (low latitudes) sustain about 70% annual mortality with net production of 2.33 juveniles/adult, whereas bobwhites in colder climates (high latitudes) sustain ≥80% annual mortality with ≥4 juveniles/adult; this relation is consistent with expected latitudinal variation in clutch size and production of birds (Ricklefs 1980, Koenig 1984). The narrow range in mean demographics of northern bobwhites does not preclude more extreme annual fluctuations. However, mean demographics tend to similar values under broad variation in climate and associated weather catastrophes, land-use practices, habitat physiognomy and floral composition, and density and composition of predator populations. To the extent that demographic processes reflect habitat quality (Van Horne 1983, Soule 1987), the narrow range might be taken as evidence for operationally similar habitat quality wherever bobwhite populations persist. This outcome has important implications in conceptualizing the population-habitat interface, as will be discussed later.

**HABITAT QUALITY**

Wildlife management in general operates under assumptions that habitat quality exists, that quality may be defined along some continuum ranging from low to high, and that population density increases as habitat quality increases. If the assumptions hold, then habitat management should be directed at increasing habitat quality.
In this section I explore the validity of 2 traditional hypotheses on the meaning of habitat quality and develop a new hypothesis that unifies empirical findings.

**The Food Hypothesis**

Applied bobwhite management has operated under the hypothesis that more food results in better habitat; that is why we have supplemental feeding, food plots, strip-discing to promote lower successional forbs (foods), and prescribed burning in certain environments. If the food hypothesis is valid, then the literature should contain evidence that food is limiting in the field and practices that increase food supplies raise average bobwhite density.

Empirical data on the availability of seeds eaten by bobwhites show high quantities relative to estimable population requirements for energy (kcals). In Michigan, seed availability in March (after winter) ranged from 1.25 to 32.5 kg/ha (Baumgras 1943). If these seeds averaged 3 kcal/g metabolizable energy (ME) and bobwhites metabolize at an arbitrarily high average rate of 50 kcal/bird-day (Case and Robel 1974, Spiers et al. 1983), then each ha potentially offered 75–1,950 bird-days of life. The Michigan sample did not include seeds on the ground (Baumgras 1943). Seeds known to be eaten by bobwhites averaged 338 kg/ha in November and December in Missouri (Korschgen 1960). Under the above assumptions on energetics, this availability translates to 20,280 bird-days/ha. Recent research in Oklahoma indicated seed production of 8.3–25.4 kg/ha on semiarid rangeland (Peoples et al. 1994), yielding 498–1,524 potential bird-days/ha. In Texas, average availability of bobwhite foods (seeds) was 1,280,176/ha in March (after winter; Doerr 1988). The empirical data on food availability do not include estimates for green vegetation, which provides limited amounts of ME (Castro et al. 1989), and invertebrates, which may be rich sources of ME (Robel et al. 1979). Neither do the data provide confirm evidence for a condition of the food hypothesis: food is limiting in the field.

If food is not limiting in the field, then it follows that practices aimed at increasing food supplies should have no effect on average density. I could not find unchallengeable, positive population responses of bobwhites to food plots in the management literature. Body fat levels of bobwhites increased in Kansas in response to food plots, which, at a minimum, would render individuals more resistant to winter weather catastrophes (Robel 1972); extra body fat would provide energy for thermoregulation under conditions of fasting or energy intake rates lower than metabolic rates. A positive density response to food plots occurred in Tennessee (Burt 1976). However, Burt’s treatments were not replicated, so the inferences pertain only to the 2 sites upon which data were collected. Although food plots were part of a management program at Remington Farms in Maryland, they were not listed as a practice responsible for population increases (Burger and Linduska 1967). Food plots had no effect on bobwhite populations in comparison with regional trends in abundance in Illinois (Ellis et al. 1969).

I found replicated data from 8 sites where supplemental feeding was tested (Table 1). These data arose from intense, experimental programs with feeders at a density of ≤25 ha/feeder and supplementation provided ≥6 months/year. The average autumn density on control sites (1.3 ± 0.33/ha [SE]) was similar to that on fed sites (1.4 ± 0.33/ha; P > 0.5). These results lead to the conclusion that food supplementation is a neutral management practice.

Bobwhite populations declined in the presence of expanding food supplies in Illinois (Vance 1976). On a 1,000-ha area between 1939 and 1974, food-producing land uses more than doubled but bobwhite density declined from 20/100 ha to 4/100 ha. Usable space declined with the removal of medium and dense fence rows and loss of interspersion.

The food hypothesis, in summary, is not so far supported by research results. This summary

---

**Table 1. Mean autumn density (no./ha) of bobwhites on control and fed areas. Feeding was not confounded with other management practices in these results.**

<table>
<thead>
<tr>
<th>Location site</th>
<th>Control</th>
<th>Fed</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Florida</td>
<td>0.25</td>
<td>0.45</td>
<td>Frye 1954</td>
</tr>
<tr>
<td>Alabama</td>
<td>0.28</td>
<td>0.28</td>
<td>Keeler 1959</td>
</tr>
<tr>
<td>Texas Rio Grande Plains</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Deep sand</td>
<td>1.73</td>
<td>1.95</td>
<td>Doerr 1988</td>
</tr>
<tr>
<td>Sandy loam</td>
<td>1.98</td>
<td>1.90</td>
<td>Guthery, n.d.</td>
</tr>
<tr>
<td>Texas Coastal Prairie</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sinton</td>
<td>0.38</td>
<td>0.25</td>
<td>Doerr 1988</td>
</tr>
<tr>
<td>Victoria</td>
<td>1.58</td>
<td>1.53</td>
<td>Kane 1988</td>
</tr>
</tbody>
</table>
statement in no way refutes the possibility that management practices that increase food supplies may be associated with increases in bobwhite populations; an example is prescribed burning under certain vegetation conditions. A food-density correlation does not necessarily imply a cause-effect relation, because food may be correlated with the independent variable that causes the population increase. Prescribed burning, for example, may increase the quantity of structurally suitable habitat (amt usable space) and improve habitat type interspersion while simultaneously increasing food supplies. Spontaneous induction of increased food as the cause of a bobwhite population response to burning is not necessarily logical.

The Interspersion Hypothesis

Leopold (1933:132) advanced the so-called law of dispersion (interspersion). The word "law" is reserved for fundamental, immutable processes in nature, so Leopold’s terminology is regrettable. Nonetheless, interspersion remains an accepted concept in habitat management theory.

Given a species such as the bobwhite, which has low mobility and requires ≥2 habitat types, the species’ density (which we take as long-term mean density) is proportional to the sum of the type peripheries (amt edge; Leopold 1933: 131–132), which we take as applying to some area of fixed size. Under Leopold’s hypothesis, we can take edge density (linear length of edge/unit area) as a measure of habitat quality. The hypothesis makes the definite prediction that, if one compares bobwhite density on any 2 areas, the area with higher edge density will support higher average bobwhite densities.

The empirical literature relevant to Leopold’s interspersion hypothesis is ambivalent. On 3 areas in Nebraska, there was a weak association between edge density and bobwhite abundance (Baxter and Wolfe 1972). Likewise, the Vance (1976) data supported the hypothesis for the same area at different times. Conversely, Hanson and Miller (1961) observed similar bobwhite density on areas with different edge densities. The interspersion hypothesis as formulated by Leopold is known to have theoretical flaws (Guthery and Bingham 1992). Their revision of the hypothesis is consistent with the limited empirical literature, i.e., the Guthery and Bingham (1992) formulation permits situations where bobwhite density bears no relation to edge density. The former circumstance (correlation exists) can occur only if unusable space exists. The latter circumstance (no correlation) occurs in the presence of redundant edge, i.e., biologically meaningful edge in excess of population requirements, in which case all space is usable.

The interspersion hypothesis of Leopold, therefore, lacks generality because of empirical and theoretical counter instances. However, some degree of interspersion must exist because of the bobwhite’s requirements for different micro- and macrohabitats and its limited mobility. Let us seek a more general definition of habitat quality that uses interspersion as a special limiting condition.

The Usable Space Hypothesis

Any bobwhite management area can be envisioned as a set of points (e.g., Cartesian coordinates) surrounded by habitat with various features. To be fully usable a point must by definition be associated with habitat compatible with the physical, behavioral, and physiological adaptations of bobwhites in a time-unlimited sense. A point meeting these conditions is given a quality value of 1, whereas a point not meeting the conditions is given a value of 0. Under this concept, the quality of the management area can be expressed as the proportion or percentage of points fully usable to bobwhites (a continuum) but quality of point-habitat does not follow a continuum. The space hypothesis makes the simple prediction that management practices aimed at increasing usable space should result in increased mean density of bobwhites.

Empirical research results are largely consistent with the space hypothesis. All of 10 habitat management practices associated with bobwhite increases in Maryland (Burger and Linduska 1967) directly or indirectly added usable space. Bobwhites increased with burning or sharecropping plus burning in Illinois because the successional stages created were favorable (Ellis et al. 1969). Creation of the appropriate successional stage maximizes usable space. However, it is inappropriate to assert that any one successional stage should be a goal of management in all geographic zones (Bailey 1984:228). The appropriate successional stage for bobwhites depends on the primary productivity of sites (Spears et al. 1993). The succes-
sional affiliation of bobwhites ranges from lower
seral stages with high primary productivity to
higher seral stages with low primary productiv-
ity. The masked bobwhite (C. v. ridgwayi) of
the Sonoran Desert can be considered a climax
species. Bobwhites may be viewed as opera-
tional constants fit to occur in habitat with rela-
tively constant structural conditions. The suc-
cessional stage that provides appropriate struc-
tural conditions changes with the primary pro-
ductivity of sites. The common denominator as
successional affiliation varies is the quantity of
usable space.

Finally, the space hypothesis is consistent
with the interspersion hypothesis as generalized
by Guthery and Bingham (1992). This assertion
can be verified by conducting a simple simul-
ation. Assume bobwhites require 2 cover types
in some area and further assume that a point in
the area is usable if it is ≤80 m (Schroeder
1985) from the 2 types. Construct a checker-
board pattern for the 2 types and gradually in-
crease the size of the squares. When the alter-
nating squares are small, all points will be us-
able under the definition as the size of the
squares increases. This means that as intersper-
sion declines bobwhite density remains con-
stant. When the squares reach some certain
size, the proportion of points usable will begin
to decline, which identifies the limiting bound
on interspersion. When the limiting bound is
breached, usable space and bobwhite density
will decline. Thus we will see situations where
density increases as interspersion increases and
where density remains constant as interspersion
increases as the Guthery and Bingham (1992)
model predicts and as has been reported in the
bobwhite management literature (Baxter and
Wolfe 1972, Hanson and Miller 1961). The data
reported by Baxter and Wolfe (1972) are con-
sistent with the space hypothesis, because bob-
white abundance was associated with the
amount of area in permanent cover (grasslands
and woodlands).

SPACE AND TIME IN MANAGEMENT
We have established the common sense re-
sult that any area of fixed size will carry more
bobwhites as the proportion of the area that
provides usable space (acceptable permanent
cover) increases. This general and somewhat
obvious outcome includes interspersion as a
special limiting condition and is consistent with
successional affiliation theory (Ellis et al. 1969,
Bailey 1984:228, Spears et al. 1993) and the re-
results of applied management research. Under-
standing of the bobwhite-habitat interface is not
complete, however, without a consideration of
the role of time.

We begin by relaxing the time-unlimited re-
striction on usability of points in habitat space.
If a point is not usable at all times, for example
a point in a wheat field that has been plowed, it
is not available in a time-unlimited sense. How-
ever, this same point might be beneficial when
it is surrounded by mature wheat or stubble.

The above reasoning leads to the concept of
usable space in time (space-time). For our pur-
poses, space-time is the sum of usable space on
each day of the year. For example, if 100 ha
were fully usable for 365 days, we would have
36,500 ha-days of space-time. However, if this
same area was subject to grazing or cropping,
the proportion of usable points would vary in
time; indeed, it is difficult to conceive of any
area consisting of fully usable points through
time.

Under the definition of management area
quality postulated above (the proportion of an
area that is usable), quality is the ratio of the
minimum amount of usable space to the total
space available during some time period. For
example, if usable space on our 100-ha area de-
clined to a minimum value of 25 ha as a result
of crop management, we could say quality of the
area is 25/100 = 0.25. This would be a good ap-
proximation for management purposes but it is
not theoretically sound.

Space-time in excess of the quantity based on
minimum available space may contribute to
population welfare via density-dependent pro-
cesses. These processes are well established in
bobwhites (Errington 1945, Roseberry and
Klimstra 1984:54,96) and other gallinaceous
birds (Potts 1986:63, Bergerud 1988:605). Be-
cause usable space and bobwhite density vary
in time, density-dependent processes may be
time-dependent. Daily survival rates might in-
crease, for example, as usable space increases
because density may decline as space increases.
The key point is that because of density-
dependent processes it is possible in principle
for an area to be of higher quality than the mini-
mum amount of usable space would indicate
(Fig. 2). Revisiting the above example, we
would say that habitat quality is >0.25 because
of density-dependent value of space in time
above the minimum amount.
Fig. 2. Concepts for understanding usable space in time (space-time). The curved line shows trends in usable space with the passage of time. Space-time above the curved line represents losses that can be addressed by habitat management. Space-time below the curved line represents the quantity available for bobwhite populations. The functional space line shows that more space is available to bobwhites than that represented by the minimum amount at any point in time because of density dependent population processes. Space-time below the dotted line represents the variable $U$, defined as functional space-time in the text.

Define functional space-time ($U$) as the quantity of space-time that contributes to standing populations on a management area during 1 year. Functional space-time takes into account the density-dependent value of space in excess of the minimum amount at any point in time. Existing density-dependent survival and production models (Johnson et al. 1993) could be used for estimation of $U$.

When one considers expansion and shrinkage of usable space in time (Fig. 2), it is apparent that any measurement of bobwhite density on an area is meaningful only relative to functional space-time. The estimate is not particularly meaningful relative to the area as a whole (crude density), because crude density varies with arbitrary definitions of area size. Consider, for example, a habitat island with a specific density of 5 birds/ha. Whereas specific density is fixed for some point in time, the corresponding crude density on an area greater in size than the island varies inversely with the arbitrary definition of area size and approaches zero as area size grows; crude density provides an irrational basis for comparing areas and developing habitat-population theory, although crude density remains acceptable as a property meaningful for management. In fact, we have developed a rather strict concept of specific density: density associated with functional space-time (space-time specific density).

Let us now consider space-time specific density relative to the general similarity in key demographic variables, discussed earlier. If crude density estimates from different sites in a region were expressed as space-time specific estimates, it is reasonable to expect that, over the long term, mean space-time specific estimates would converge to similar values on different areas. Convergence follows because populations are subject to similar survival-production schedules, density dependence, and frequencies and severity of weather catastrophes within regions. Regional synchrony in demographic variables is known in nongame birds (Bohning-Gaese 1994). These arguments support use of a constant of proportionality, which is in fact space-time specific density, in the following conceptual model of crude density as a function of space-time:

$$D_g = \begin{cases} k_g U, & U \geq M_g \text{ and } T \\ 0, & U < M_g \end{cases}$$

(4)

$D_g$ = long-term average (crude) density (no./ha) on a management area on some arbitrary annual date in geographic region $g$.$k_g$ = space-time specific density (no./ha$^2$-day) for some arbitrary annual date in geographic region $g$.$U$ = functional space-time (ha-days) annually available on a management area (defined above),$T$ = total space-time (ha-days) annually available on an area (e.g., the product of area size in ha and time in days), and$M_g$ = the quantity of space-time (ha-days) annually required for a minimum viable population in geographic region $g$.

The annual period implicit in subsequent discussion is autumn to autumn.

Equation (4) gives crude density as a segmented function of functional space-time. The limiting conditions in the top segment indicate that some minimum amount of space-time is required for a viable population and that crude density cannot exceed mean density in fully usable space (all points available at all times). The bottom segment indicates that the long-term average value of crude density will be zero if there is not enough functional space-time for a viable population.

The constant of proportionality, i.e., space-time specific density, is the ratio of long-term
mean density (no./ha) in fully usable space to total space-time annually available on an area (T). The unit of measure for the constant is number per ha-squared-day (no./ha²-day). Multiplication of the constant by functional space-time yields density in no./ha. The constant will take small values in general. For example, if an area supports a mean autumn density of 2.5 birds/ha and all space is usable at all times, the constant is 0.00685/ha²-day.

Equation (4) may be viewed as a generalization of the law of dispersion (Leopold 1933:132). The equation contains 2 of the same variables as the Guthery and Bingham (1992) formulation of the law (D, k) while incorporating the usable space provided by edge (Giles 1978:136) and a consideration of time. The constant k in Leopold’s law has the units no./l³ where l is some unit of length. The conceptual model differs from the law of dispersion by forcing one to think simultaneously of the relations among bobwhite density and habitat space in time (history) and by imposing limits on the range (dependent variable) and domain (independent variable).

Subscribing the constant of proportionality to a specific geographic region is also a consideration of time in the habitat-population interface. The frequency and severity of weather catastrophes (droughts, blizzards, heat waves) vary among regions; the effects of such catastrophes on bobwhite production and survival are common knowledge. Suppose a population suffers a catastrophe such as extended snow cover and freezing temperatures, which decimates numbers. Suppose that after the catastrophe, the birds are awash in resources and no further catastrophes ensue. Because populations grow at time-based rates, we can say the post-catastrophe population is time-limited, at least in the near term. In other words, given the same average annual amount of functional space-time, a population exposed to more frequent, more severe catastrophes may have a lower average space-time specific density than one exposed to less frequent, less severe catastrophes (Fig. 3). Variation in the frequency and severity of catastrophes among geographic regions affects the constant of proportionality in equation 4 (Fig 3). Areas may have identical, nonlimiting habitats and different average bobwhite densities during some relatively short time horizon (e.g., 10–50 yr).

If we could somehow remove the effects of catastrophes and time on long-term average densities, we would have the remarkable possibility that a general constant of proportionality (k) would hold throughout the geographic range of bobwhites. A general constant implies that long-term average density in functional space-time would be roughly constant everywhere, given that a population was neither increasing nor declining through time. Whereas this assertion seems preposterous at first reading, one must remember that the bobwhite is more or less a biophysical constant throughout its vast geographic range (Johnsgard 1973:413). The demographic potential of subspecies is similar as evidenced by the preceding section on demography.

Equation (4) also provides an explicit management goal, namely, practice habitat management on any area such that

\[ U/T = 1. \]  

Equation (5) is a succinct way of stating that habitat managers should strive to obtain usability of all points in space at all times. Other ways of stating the goal are that managers should strive for space-time saturation on any management area, or they should provide bobwhite populations the opportunity for unconstrained use of space through time. The various expres-
sions of the goal are common sense outlooks that seem to have been obscured by unjustified concerns over foods, edge, and interspersion and the lack of a general understanding of successional affiliation. When a manager has saturated an area with space-time, no further habitat management is necessary.

APPLICATION OF THE CONCEPTUAL MODEL IN MANAGEMENT

The conceptual model (eq 4) and the ideas used to develop it provide a formal method of thinking about the bobwhite-habitat interface and that method of thinking is the primary applied benefit of the model. The model could serve as a basis for evaluating quality of an area (as defined), identifying habitat problems in time and space, predicting the outcomes of management activities, and evaluating whether remedial management is feasible. The quantity of usable space on a management area should be considered a dynamic variable and followed through time. For example, a set of sample points could be evaluated monthly. Trends in the proportion of points that are usable, given associated habitat features and a minimum interspersion bound, provide information on trends in habitat quality (proportion of space that is usable) on the area. These trends identify periods of reduced usable space and field observations will identify the causes of the reduction. Estimation of the mean number of bobwhites on the area, when expressed in terms of the minimum amount of usable space (specific density), provides data for estimating $k_g$. If mean specific density is $d$, then

$$k_g \equiv d/365 \quad (6)$$

and

$$D_g \equiv \begin{cases} 365 \frac{k_g A_m}{A} & A_m \geq A_g \\ 0 & A_m < A_g \end{cases} \quad (7)$$

where

$A_m =$ the min. amt of usable space during 1 yr (ha),
$A =$ the size of the area (ha), and
$A_g =$ the amt of space (ha) required for a min. viable population.

As an example, suppose an area has 650 ha. An audit reveals that usable space declines to 200 ha in late summer; the area holds an average of 250 birds in autumn. From these data, we estimate

$$d = 250/200 = 1.25,$$

$$k_g \equiv 1.25/365 = 0.0034,$$

$$D_g \equiv 365(0.0034)(200)/650 = 0.38,$$

and

$$U/T \equiv A_m/A = 200 \text{ ha}/650 \text{ ha} = 0.31.$$  

The above values provide a basis for estimating population response to habitat management that increases the minimum amount of usable space at any point in time. Note that if my interpretation of the literature is correct, management aimed at improving the quality of the area $A_m$, i.e., the area that already is fully usable in time, will not affect crude density, specific density, or population size. Note also that if the area is approximately saturated with space-time ($A_m/A = 1$), there may be no point in doing habitat management.

There is a large descriptive literature from which management biologists can determine the usability of points in the space available on a management area. Summary references include Stoddard (1931), Rosene (1969), Lehm (1984), Roseberry and Klimstra (1984), Schroeder (1985), and Guthery (1986).

TESTABLE ASSUMPTIONS AND PREDICTIONS

If my interpretations of and extrapolations from the bobwhite literature are correct, then certain implicit and explicit assumptions and predictions arise from the arguments. These assumptions and predictions are amenable to field tests.

An important implicit assumption is that carrying capacity for bobwhites is not necessarily a property of land, given the land is saturated with space-time. Rather, carrying capacity, as reflected by, e.g., a moving average from a time series on density (Roseberry and Klimstra 1984:124), is a property of frequency and severity of weather catastrophes, density dependent production and survival, and time. If this concept of carrying capacity holds, then field experimentation will be able to demonstrate the existence of areas with functionally nonlimiting habitat resources and significantly different mean bobwhite densities over time. The above prediction holds only with space-time saturation on experimental areas or with densities expressed in a space-time specific format.

The general nature of the arguments leading to equation 4 compels a hypothesis on weather catastrophes that operate on production as well as survival. The devastating effects of severe
winter weather on survival are common knowledge. Summer deluges are known to be damaging to production (Stoddard 1931:185, Rosene 1969:145). A poorly understood but potentially powerful explanation for variation in production is heat at quail level. The damaging effects of drought and high temperatures on bobwhite production are documented in Missouri (Stanford 1972). High daily temperatures in July and August may reduce the effective laying period up to 45 days (Klimstra and Roseberry 1975) with consequent effects on renesting and production. In summary, the management philosophy requires a non-food basis for variation in production; heat loads exceeding reproductive tolerance may provide that basis.

The concept that a point in habitat space is either usable (quality = 1) or unusable (quality = 0) at any time is amenable to testing. Study areas with substantial variation in habitat variables (e.g., bare ground exposure, herbaceous vegetation biomass, woody canopy coverage) near points need to be selected. Then data on habitat variables need to be collected at points where bobwhites occur and at randomly available points. From these data, one may construct continuous selection ratios (use/availability; Appendix). If a plot of the continuous selection ratio against the value of a habitat feature has steep sides with a flat top, the binomial concept of point habitat quality is supported. Otherwise, the binomial concept is refuted.

A final prediction is that management aimed at increasing food supplies or increasing interspersion on areas saturated with space-time will fail to increase mean density. Equation (4) is based wholly on usable space in time; food is not a consideration because past results do not support the food hypothesis and interspersion serves only to set a limiting condition on space usability.

RESEARCH NEEDS

If we envision a management area as a set of points either usable or unusable at different times, then we need a comprehensive theory of the properties of usable points (note that usability of a point must be considered in the context of a small area surrounding the point). In short, we need a comprehensive theory of point habitat.

Species-habitat models for bobwhites provide an established approach for developing the theory. However, existing models (Schroeder 1985, Bidwell et al. 1991, Rice et al. 1992) suffer shortcomings when viewed in composite. For example, the suitability indices for habitat features such as bare ground exposure vary markedly among authors. Moreover, habitat suitability indices usually are based on subjective opinion rather than empirical data. There is a need for descriptive research on the properties of points at which bobwhites occur relative to the properties of randomly available points, again recognizing that nearby habitat determines the usability of a point.

To obtain a fundamental understanding of point usability in time, we must, as a research community, take the question to the proper depth relative to the physical, behavioral, and physiological adaptations of bobwhites. The physical question is relatively straightforward: the size, strength, and mobility (walk, fly) of bobwhites clearly limit their occurrence to points with certain structural properties and distance (interspersion) relations. The behavioral question is more challenging. Do bobwhites, via evolutionary perceptions, limit their occurrence to points in space that permit largely unrestricted exercise of predator-avoidance mechanisms? There is some evidence that the answer is affirmative with regard to flight space (Kassinos 1994). Finally, the question of the properties of a point relative to physiological adaptions has to do with heat flow and thermoregulation. The question to be answered is, does the point have thermal properties (air temp, ground temp, wind speed, irradiance) through a year consistent with a bobwhite’s thermoregulatory abilities? Goldstein (1984) provides an example of needed research.

CONCLUSION

Results from 60 years of research on demography and habitat management provide a common-sense model of the bobwhite-habitat interface. I have added weather catastrophes and time as important dimensions for understanding and interpreting the interface; without consideration of catastrophes and time, bobwhite population variables (density, survival, productivity) may provide misleading indicators of habitat value.

The concepts of space-time and functional space-time provide omnibus variables for evaluating management treatments. Space-time can be audited under any management treatment that alters the structure and physiognomy of
habitats, such as grazing systems, brush management patterns, and land-use patterns. Perhaps the lack of an omnibus response variable has impeded development of theory in bobwhite habitat management.

The research community should challenge my interpretations based on the testable assumptions and predictions provided as well as on deductions the community develops. If the habitat management model (eq 4) withstands challenges, past research has led to useful generalizations. To the extent that the model can be falsified, we gain reliable knowledge and make progress towards a strong theoretical basis for management of bobwhite habitat.

MANAGEMENT IMPLICATIONS

The goal of habitat management for bobwhites should be to make all points on an area usable by bobwhites at all times. When this goal is achieved, the manager has given bobwhite populations the opportunity for maximum expression of demographic potential; no further habitat management is expected to increase densities. Managers must realize that bobwhite populations will show considerable annual variability with space-time saturation due primarily to the frequency and severity of weather catastrophes.

LITERATURE CITED


Received 22 August 1995.
Accepted 16 October 1996.

Associate Editor: O’Connor.

APPENDIX

In this appendix, I briefly describe the mathematical background for testing the hypothesis that points in habitat space are either usable or not usable by bobwhites. Consider a single habitat feature, e.g., canopy coverage of brush, which may be measured relative to points at which bobwhites occur and to randomly available points. Manly et al. (1993:40–41) provide theory for the discrete case (arbitrary classes for a habitat feature) from which a selection ratio may be calculated. The ratio is proportional use/proportional availability.

Arbitrary classes may be eliminated by modeling the selection ratio as a continuous function of values of a habitat feature. With field data it is possible to model cumulative frequency distributions for used points, $F(x)$, and for random points, $G(x)$. Banks (1994) provides several models for cumulative distribution functions and methods of estimating parameters. The functions may be interpreted as cumulative relative frequency of observations at the value $x$ of a habitat feature under consideration. Differentiating the cumulative distribution functions results in probability density functions (Mendenhall et al. 1990:144–145), $f(x)$ and $g(x)$, respectively. The continuous selection ratio, $u(x)$, may now be defined as

$$u(x) = rac{f(x)}{g(x)}, \quad g(x) > 0.$$