

FIELD EVALUATION OF THE NORTHERN BOBWHITE HABITAT
SUITABILITY INDEX MODEL WITH IMPLICATIONS FOR THE
CONSERVATION RESERVE PROGRAM

by

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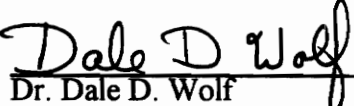
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(ABSTRACT)

A field evaluation of a modified version of the northern bobwhite (Colinus virginianus) Habitat Suitability Index (HSI) model was conducted using habitat and relative abundance data from 121 sites distributed throughout Halifax County, Virginia, 1986-1991. Model output and the index of relative abundance were only poorly correlated ($r_s = 0.09$, $P = 0.31$, $n = 121$). The model identified winter food as the limiting factor at 115 of the 121 sites. However, the Composition Suitability Index for the equivalent percent of the station providing winter food in optimum condition and the performance measure were not correlated ($r_s = 0.09$, $P = 0.33$, $n = 121$). Population performance at 49 of the 115 sites exceeded levels indicated by the model. Attempts to improve the fit of the model focused initially on the winter food component of the model. Attempts to improve the fit of the model by considering alternative food sources, the role of habitat interspersions, the individual variable Suitability Index curves, and a reassessment of the contribution of crop fields to the

estimate of available winter food were unsuccessful. Quail appeared to be nest/brood habitat rather food limited. The index of quail abundance and the estimate of available nest/brood habitat were correlated positively ($r_s = 0.55$, $P < 0.001$, $n = 121$).

Winter habitat use within the covey home range was evaluated January through April of 1990 and 1991 by comparing micro-habitat conditions at used and unused sites within the home range. Two different statistical treatments (regression and signed-rank) were used to determine if preferential habitat use was occurring. Whereas the signed-rank test yielded significant ($P = 0.04$) results for only 1 of 7 micro-habitat parameters, results from the regression analyses were all significant ($P < 0.05$), indicating disproportional use of habitat characteristics.

The potential effect of the Conservation Reserve Program (CRP) on northern bobwhite populations was evaluated by comparing nest/brood habitat conditions in crop and 4 CRP field types including CP1, CP3 < 8 yr, CP3 > 8 yr, and CP3 fields receiving some level of commercial thinning. Short-term effects are likely to be positive. Both CP1 and CP3 field types should provide more suitable nest/brood habitat conditions than crop fields. Long-term effects of the CRP on northern bobwhite are likely to be negative. Conservation Reserve fields with pines (CP3) > 8 yrs old provided virtually no nest/brood habitat. Commercial thinning did not appear to have a positive impact on habitat conditions.

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INTRODUCTION

NORTHERN BOBWHITE POPULATION STATUS

In 1992, researchers, managers, and others with an interest in the 6 species of North American quail convened in Kansas City, Missouri for the 3rd National Quail Symposium. Although a diversity of research topics was presented, 2 themes were consistent throughout: 1) at the present rates of decline, huntable populations of northern bobwhite (*Colinus virginianus*) will disappear throughout much of the species' range, possibly as soon as the year 2000 (Brennan 1991) and 2) we know disturbingly little about even the most basic aspects of the species' biology and life history, despite nearly 70 yr of research (Brennan 1993). As Brennan (1991:554) stated, "The irony [of this situation] is nearly unfathomable because effective habitat management techniques for the bobwhite have been known for over a half century." Land use changes and habitat loss notwithstanding, it seems that either our foundation has been based on unreliable knowledge (Romesburg 1981) or we have misled ourselves into believing that we know much more than we actually do (Gill 1985).

Brennan (1991) summarized Christmas Bird Count (CBC) data and Breeding Bird Survey (BBS) data (Droege and Sauer 1990) and concluded that bobwhite population declines have been significant in 77% of the states within the species'

range. These declines have been most dramatic in the southern region of the bobwhites' range, an area considered to be typified by both good quail habitat and management. Harvest data and population trends in Virginia are consistent with these findings.

Fies (1992) speculated that quail populations have been declining in Virginia for ≥ 50 years. Breeding Bird Survey data (Droge and Sauer 1990) for Virginia indicated that populations have been declining since at least 1966. The number of quail detected on BBS routes decreased nearly 42% from 1966 to 1990. Harvest trends during this period are consistent with these data. Virginia Department of Game and Inland Fisheries data revealed that harvests of bobwhites decreased by 84% (Gywnn, unpubl. data). Success data (quail bagged/hour) for the period from 1949 to 1990 declined by 55% (Fies, unpubl. data). However, although these harvest data are consistent with population trends, and seemingly convincing as an indicator of northern bobwhite population trends, Stauffer (1993) cautioned against a strong reliance on harvest trend data, principally because of the variable nature of the source and the general lack of quality control from a statistical perspective.

HISTORY OF AGRICULTURAL LAND USE

Researchers believe that habitat loss and the modification and fragmentation of remaining habitat have been the primary factors responsible for declining quail

numbers (Roseberry 1979, Roseberry and Klimstra 1984, Brady 1988, Brennan 1993, Kuvlesky et al. 1993). Despite a lack of manipulative experimentation, the nearly simultaneous declines in quail populations and other farmland species and modernization and mechanization of the agricultural industry, suggests a causal mechanism for such declines.

From 1935 to 1982, the number of farms in the U.S. declined from 6.81 million to 2.24 million (Edwards et al. 1985). During this period, there was little change in the total acreage farmed, simply a redistribution of farms by size class. Since 1925, the number of farms between 20-105 ha has declined nationally. Mid-sized farms (105-202 ha) were increasing until the mid-50s, at which time a downward trend began (Edwards et al. 1985). Trends in the Midwest and South were similar. From the early part of the 20th century until 1982, there was nearly a 50% reduction in the number of farms in Iowa. Again, this loss was not evenly distributed among all farm sizes. Farms 20-202 ha in size decreased by 58% while farms > 202 ha increased 848% (Lasley 1987). Fies (1992) reported a similar trend for Virginia. The total number of farms decreased from 151,000 in 1950 to 44,779 in 1987, a decline of nearly 70%. The majority of the farms lost were small (<20 ha) and medium-sized (20-200 ha) farms. This loss represents nearly a 45% drop in total acres farmed. Average farm size however, increased 88% during this period

from 42 to 79 ha. Many farms lost were small tenant farms, a pattern noted in Mississippi as well (Brennan 1991). During the period from 1942 to 1982, the total number of farms in Mississippi decreased from 291,092 to 42,415 and mean farm size increased from 22 ha to 118 ha. The potential negative impacts on farmland wildlife notwithstanding, these changes in farm size were inevitable following the post-World War II mechanization of the farming industry. Faster, more efficient means of farming allowed the producer to farm more hectares, while advances in plant breeding, transportation, and sophisticated farm machinery (Papendick et al. 1984) led to the regionalization of the agricultural industry. Both factors, while encouraging larger fields on larger farms and increases in short-term profits, compromised some of the most valuable wildlife habitat. Increases in both machinery and field size came at the expense of fencerows and areas once viewed as only marginally productive [headlands (areas at field-ends for turning equipment), wet spots, and so called "odd areas"]. These areas were obstacles to using large equipment (Burger 1978, O'Connor and Shrubbs 1986). However, as Leopold (1933), Burger (1978), Brokaw (1978), the National Research Council (1982), and Cacek (1984) noted, these areas are some of the most productive habitats for wildlife. They provide food and cover and serve as travel lanes for many farmland species.

IMPACTS OF LAND USE CHANGE ON WILDLIFE

As a result of changes in the farming industry, declining wildlife populations were being observed throughout the U. S. Vance (1976) attributed the extirpation of the prairie chicken (Tympanuchus spp.) and a 78% reduction in the northern bobwhite population in Illinois to the loss of edge, grass and nesting habitat, and fencerow cover. Steavenson et al. (1943) found that fields with unkempt borders were capable of supporting 60% more pheasants (Phasianus colchicus) than fields with clean borders. Additionally, they reported that cleanly-farmed areas had smaller songbird populations than areas where fencerows prevailed. Leedy (1940) pointed out that fencerows served as excellent sources of food and cover and as valuable travel lanes for pheasants. He stressed that brushy fencerows were used 3000% more by pheasants than clean fencerows. Warner et al. (1984) suggested that the move to intense agriculture was responsible for significant declines in ring-necked pheasant chick survival rates between 1946 and 1981. Warner et al. (1987) stated that the increase in row crop production in the late 1960s and early 70s resulted in a significant decline in the pheasant population in Illinois.

Agricultural specialization, generally a result of sophisticated farm machinery, advances in plant breeding, and rapid transportation (Papendick 1984),

has negatively impacted farm wildlife. Cacek's (1984) investigation of organic farming and its potential impact on farm wildlife revealed the importance of crop diversification. In comparing organic farms in eastern Nebraska to adjacent conventional farms, he found 800% more bird territories on the organically-farmed areas. He attributed this disparity to the greater habitat diversity provided by the crop rotations in organic farming. Leite (1971) demonstrated the detrimental effects of reduced crop rotations on pheasants. Eliminating the legume cover crop often associated with 5-6 year rotations dramatically reduced the amount of superior nesting cover available for pheasants. Papendick et al. (1984) pointed out that the primary advantage of organic farming for wildlife are the longer crop rotations than under conventional systems. They concluded that wildlife generally benefit from organic farming systems because crops are more diverse than on conventional farms and thus offer a mixture of habitats.

IMPACTS OF LAND USE CHANGE ON NORTHERN BOBWHITE

Northern bobwhite populations have been equally affected by "clean farming" and associated specialization. As Roseberry and Klimstra (1984) noted, the bobwhite's daily and seasonal needs are met by a variety of cover types which, because of the species' limited mobility, must be in close proximity to each other.

Subsequently, the species is limited to areas of high habitat diversity resulting from the proximity of small patches of habitats meeting the species' needs, landscapes typical of old-fashioned farming systems. The changing agricultural industry has eliminated many of these once typical farming units (Roseberry and Klimstra 1984). From 1939 to 1948, Goodrum (1949) found "clean" farming and increased livestock production to be the 2 primary factors responsible for a nationwide decrease in quail numbers. Brady (1988) reported that declining harvests of bobwhites were associated with increasing area of row crops in Illinois over a 30-yr period. These broad scale changes in land use have eliminated hundreds of thousands of kilometers of weedy fence rows and millions of ha of small fields that once provided prime nesting and brood-rearing habitat for the bobwhite (Klimstra 1982). Clean farming practices and silvicultural systems that maximize basal area are 2 of the most likely causes of habitat loss and subsequent decline in bobwhite populations (Brennan 1991). The large fields and monocultures typically associated with modern agriculture are much less suitable as quail habitat (Roseberry and Klimstra 1984).

Church et al. (1993) suggested that declines in northern bobwhite populations are the result of changes taking place on the agricultural landscape. The authors examined long-term (1966-1991) BBS data for a grassland/shrub guild comprising 13 species of passerines sympatric with the bobwhite. Although not statistically

significant, they found that > 50% of the 13 species showed declining populations similar to the bobwhite in 23 of 26 states examined. As Klimstra (1982) noted, current land-use practices simply do not provide habitat for the bobwhite.

The northern bobwhite is no longer a by-product of the farming industry. That they require early-successional habitats frequently disturbed by fire or mechanical means implies that any attempt to preserve, restore, or enhance populations will undoubtedly come at a cost to resource agencies. Less certain however, will be the success of these efforts. While Brennan (1991) believed that when appropriate habitat management is applied, bobwhite populations will almost certainly respond, others are less optimistic. Church and Taylor (1992) argued that, habitat loss notwithstanding, much of the current situation regarding the bobwhite is due to what Gill (1985) called "arrogance of ignorance." Specifically, Church and Taylor (1992:793) contend that the situation faced by the bobwhite is a direct result of the fact that the outlook of many has been one of "...our knowledge of bobwhite biology and ecology is relatively complete and little can be done to enhance existing programs." In contrast to the opinion of Brennan (1991) they pointed out that, "Recent emphasis on habitat has served to highlight what little is really known about the life history and requirements of the bobwhite in today's environment (Church and Taylor 1992:793)." They later restated their concern, pointing out that their

1992 results "...indicate that there is reason to question the efficacy of current management practices for bobwhite and scaled quail (Church et al. 1993:54)." This sentiment was echoed by many who presented management and research findings at a recent national symposium devoted to the management and research of the 6 species of quail native to the U. S. DeVos and Mueller (1993:89) contended that, "brood habitat is rarely defined because individual components of quality brood range are relatively unknown." Moreover, they note that, despite 50 years of research, there is little knowledge of breeding season ecology and habitat use. Others, including Suchy and Munkel (1993) and Curtis et al. (1993) and Burger et al. (1995) felt similarly about the reproductive biology of the species and the lack of knowledge of factors that influence seasonal variation in survival and mortality factors, respectively. Robel (1993) questioned how we can even begin to determine the quality of a given habitat when we do not understand the macro- and micro-nutrient needs of the quail. We know very little about the role of predation and the effects of hunting (Brennan 1991, Burger et al. 1994). Surprisingly, this situation exists despite nearly 70 years of research and over 2,800 titles published on the life history and management of the bobwhite (DeVos and Mueller 1993). Some believe that habitat relationships is an area deserving the most attention because of the paucity of scientifically-based information (Brennan 1991).

In 1987, the U. S. Fish and Wildlife Service took the opportunity to not only potentially fill some of these knowledge gaps, specifically those associated with habitat relationships, but also evaluate the potential for improving quail habitat via the Conservation Reserve Program (Farmer et al. 1988). The evaluation of the impact of the CRP on quail habitat was to be based on a modified version of the northern bobwhite HSI model. Although the model is the most comprehensive source of quantitative data on northern bobwhite habitat use, the model has yet to be evaluated. Given this, and the paucity of quantitative data on northern bobwhite habitat use, the objectives of this study were 1) evaluate the predictive ability of the Habitat Suitability Index model for the northern bobwhite as a model of potential population performance and if necessary, provide recommendations for improving the model, 2) use the results of the model test in conjunction with an evaluation of local micro-habitat conditions to evaluate the potential impact of the CRP on local quail populations and 3) describe winter micro-habitat use patterns of northern bobwhite.

STUDY AREA

This study was conducted in Halifax County, Virginia (Fig. 1). Relief is nearly level along streams and rolling to gently rolling on the ridges. Elevations

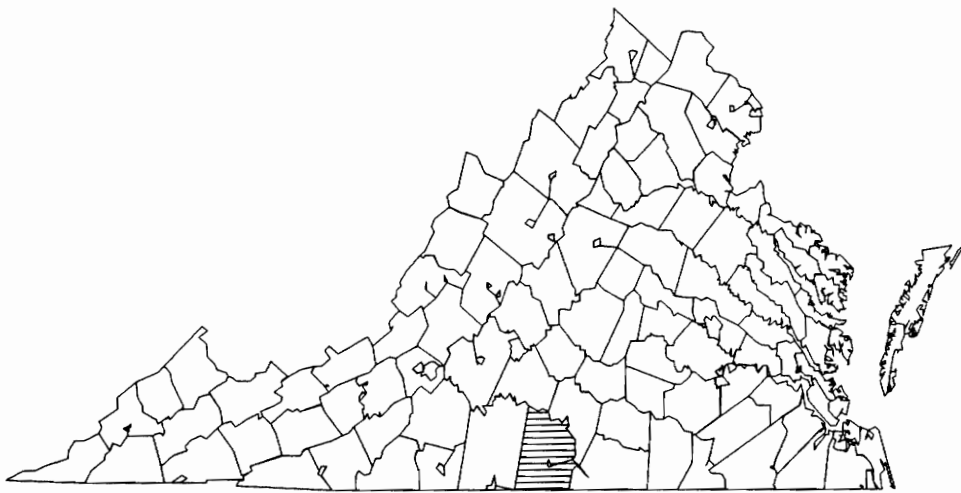


Figure 1. Study area location for the field evaluation of the northern bobwhite HSI model, Halifax County, Virginia.

range from 90 to 180 m. Mean daily temperatures range from 3 C in January to 26 C in July (Virginia Crop Reporting Service 1982).

About 66% (140,580 ha) of the county is forested (Center for Public Service 1992). Common woodland trees included oaks (Quercus spp.), yellow poplar (Liriodendron tulipifera), hickories (Carya spp.), ashes (Fraxinus spp.), sweetgum (Liquidambar styraciflua), loblolly pine (Pinus taeda), Virginia pine (P. virginiana), dogwood (Cornus spp.), and sassafras (Sassafras albidum).

Mean annual production of small grains, tobacco, and soybeans accounted for 26, 18, and 14% of the open cropland, respectively (L. White pers. commun., Halifax County, Va., SCS). Mean farm size and mean field size were 78 ha and 1.7 ha, respectively (Center for Public Service 1992).

CHAPTER 1: NORTHERN BOBWHITE HABITAT SUITABILITY INDEX (HSI) MODEL EVALUATION

INTRODUCTION

Nearly a decade of heightened environmental awareness and a revolution in the perception of wildlife and its management by all Americans were primary driving forces behind the National Environmental Policy Act (NEPA) of 1969 (Thomas 1982). Its directive was simple - no federally-funded land or water resource development project was to begin until an evaluation of the project's potential impact on the environment, including terrestrial and aquatic wildlife, was complete. With the passage of the act, those charged with the responsibility of managing those natural resources that spawned the act, realized that the need for a systematic and standardized approach for evaluating a project's potential impacts was as great as the need to protect such resources. This need was met, at least in principle, with the development of several standardized protocols, of which the Habitat Evaluations Procedures (HEP, U.S. Fish and Wildlife Service 1980a) was probably the most significant for wildlife, in terms of its potential for use.

Despite their purpose, NEPA in particular, and other federal environmental legislation in general, provided little guidance for impact assessment. These acts

were consistent however, in that each acknowledged that any approach would have to reflect the fact that various interests perceived environmental resources quite differently, e.g., species-populations, biological integrity/ecosystem function, and habitat (U. S. Fish and Wildlife Service 1980b). Their differences notwithstanding, it was generally recognized that each view was ultimately linked in some manner to ecosystem function, which could be evaluated via energy flow, population estimation, or habitat. Of the 3, energy flow was viewed as the most scientifically sound, but least practical. Because HEP was being developed primarily for use in water development studies (Farmer, unpubl. data), and habitat variables seemed to be reasonable indicators of wildlife response to water development, a habitat approach to assessment was adopted by the U.S. Fish and Wildlife Service. Moreover, an assessment of habitat, unlike a census of species populations likely to be impacted, was much easier to implement, typically includes variables likely to be directly affected by the project (Pajak and Neves 1987), and was much more consistent with fiscal and time constraints associated with such projects. Further, most federal agencies manage habitats, not species (Schamberger and Krohn 1982) and since, as appropriately stated by Anderson (1991) "...habitat is what enables species to exist," the HEP was developed.

HABITAT EVALUATION PROCEDURES

HEP has been referred to as an "accounting system for determining the quality and quantity of fish and wildlife habitat" (Wakeley 1988:79). A HEP evaluation consists of identifying the area to be impacted or serve as a mitigation site, estimating its size, and generating an estimate of the potential (this is a necessary consequence of using habitat as the basis of a *quality* assessment, see below) quality of the site for selected evaluation species. The quality (Habitat Suitability Index, HSI) and quantity (area) dimensions are combined in a multiplicative function, yielding what has been termed, "a currency for wildlife" (O'Neil 1993:1), the Habitat Unit (HU):

$$\text{HU} = \text{HSI} * \text{Area}$$

It is assumed that the HSI shares a linear relationship with carrying capacity or some other measure of population performance.

The concept of carrying capacity accounts for all the environmental factors that limit wildlife populations. Because habitat is a subset of these factors, it is assumed that model output is an index of the potential (actual carrying capacity is likely to be influenced by a multitude of factors external to the model) carrying capacity (Farmer et al. 1982). More specifically, it is assumed that the relationship

between model output and carrying capacity is linear, or can be converted to a linear relationship (Terrell 1984). Consequently, because carrying capacity is typically expressed as individuals per-unit-area (Farmer, unpubl. data), model output then implicitly expresses the potential of a site on a per-unit-area basis. The simplicity of HEP is attractive. Its acceptance however, has not been universal, principally because of skepticism concerning the HSI models. However, much of this concern has evolved from inappropriate applications of these models and a general lack of understanding of their purpose.

HSI Models

Overview

Morrison et al. (1992) generally classified habitat models as either theoretical, which include both descriptive and mathematical, or empirical. They identified 2 types of empirical models, statistical and descriptive. The distinction between these model types is one of degree. While both types of empirical models are based on observation, descriptive models are much less rigorous with respect to data and statistical treatment. Most wildlife habitat models are empirical. HSI models however, are considered by some to be theoretical in nature because the relationships between model output and each environmental variable in the model

are assumed, rather than derived from field observations (Morrison et al. 1992).

Although HSI model developers may draw on expert opinion and other types of less rigorous observational data sources, the use of empirical data does not separate HSI models from statistical habitat models. The principal distinction is in the assumed precision of model output.

HSI model output is a unitless index ranging from 0 to 1, where habitats assigned a 0 are assumed to be completely unsuitable, while those receiving a 1 are assumed to be optimal. The unitless index is a consequence of the fact that multiple sources of data, using a range of quantitative measures of population performance, are typically used in the development of HSI models.

Development

The basis for HSI model development rests on the following assumptions: 1) habitats have an intrinsic carrying capacity for a given species, 2) physicochemical and structural aspects of the habitat can be related to carrying capacity, and 3) a group of the most important habitat-carrying capacity relationships can be identified and incorporated into a simple model (Bain and Robinson 1988). Within this framework, model development begins with setting objectives for the model. This may include determining the acceptance level for model output and defining the

geographical area for which the model is to be valid. Acceptance levels for model output may range from agreement with rankings of an expert opinion to more precise measures such as predicting population size within some predetermined limits. Variable selection and the development of hypotheses that relate each variable to population performance then follow.

Variable selection begins by identifying components such as seasonal habitat, or life requisites such as food and cover, that are known to be potential limiting factors for the species under consideration. Once these life requisites are identified, individual variables are selected to represent each life requisite. Next, the presumed relationship between each variable and habitat quality (measure of population performance being used) is operationally defined. This process yields individual variable Suitability Index (SI) curves. These curves represent working hypotheses about each variables' potential contribution to habitat quality. Like model output, these SIs range from 0 to 1. In those cases where more than a single variable is used to describe a life requisite, the developer must define how these variables are to be aggregated mathematically to represent the life requisite. An implicit assumption is that the variables composing the life requisite are not correlated. As with the individual variables, a hypothesized relationship between each life requisite or habitat component, and habitat quality is then formally established as a Life

Requisite Suitability Index (LRSI). For those models that evaluate quality for a single life requisite or habitat component such as reproductive habitat, model output is equal to the LRSI. In those cases where more than a single life requisite is considered, model output is typically equal to the smallest of the LRSIs.

Northern Bobwhite HSI Model

Northern bobwhite population levels are determined principally by the extent of overwinter mortality and annual recruitment into the population (Klimstra and Roseberry 1975). Therefore, Schroeder (1985) assumed that an assessment of the availability of winter food and protective cover, as well as the availability of brood rearing and nesting habitat, would adequately describe the species' annual habitat needs. The HSI model for the northern bobwhite (Schroeder 1985) contains 15 variables, representing winter food, cover, and nest/brood habitat.

The draft HSI model by Schroeder (1985), which was based on the literature and review comments of 9 individuals considered northern bobwhite experts (O'Neil 1993), was modified for use in a nationwide evaluation of the Conservation Reserve Program being conducted by the U.S. Fish and Wildlife Service (Farmer et al. 1988). The modified version, hereafter referred to as the CRP HSI model, contains 8 variables. Four variables describe the winter food life requisite and 3 represent

nest/brood habitat. A single variable represents the cover needs of the species (Table 1).

Individual Variable Suitability Indices

Winter Food Life Requisite. — The primary foods of the bobwhite have been identified as wild seeds (primarily annual forbs), legume seeds, cultivated grains, mast, fruits, grass seeds, and insects (Edminster 1954). In their review of 27 food habits studies, Landers and Johnson (1976) identified > 650 seed types consumed by the bobwhite. Of the food types identified, 78% composed 1% or more of the food volume in ≥ 1 study. Beggarweeds (*Desmodium* spp.), ragweeds (*Ambrosia* spp.), lespedezas (*Lespedeza* spp.), corn (*Zea mays*), soybeans (*Glycine max*), cowpeas (*Vigna* spp.), partridge peas (*Cassia* spp.), oaks (*Quercus* spp.), and pines (*Pinus* spp.) were among the food types comprising a high percent frequency and volume. During winter and early spring, there are generally 3 potential sources of food for northern bobwhites: crop residues, seeds from herbaceous plant material, and mast from pine and/or oaks. The density of mast producing trees > 25.4 cm dbh, percent canopy cover of herbaceous quail foods, and percent canopy cover of late-winter quail foods are used to evaluate northern bobwhite winter food resources (Table 1, Fig. 2).

Because the bobwhite tends to fly only when forced to do so, the density of

Table 1. Number, description, and abbreviated names for 8 variables composing the CRP Habitat Suitability Index (HSI) model for the northern bobwhite.

Variable Number	Description	Abbreviated Name ¹
WINTER FOOD		
1	% canopy cover of late-winter quail foods	cclwf ²
2	% canopy cover of preferred bobwhite herbaceous food plants	x104v1
3	% of ground that is bare or covered with a light litter layer	grndfd
4	density of pine or oak trees > 25.4 cm dbh/ha ³	vdndb01
COVER		
5	% canopy cover of woody vegetation 0.5 - 2 m high ⁴	cc5_2
NEST/BROOD		
6	% of the herbaceous canopy that is composed of grasses	vrcgr01
7	% herbaceous canopy cover	vcvhe01
8	% of ground that is bare or covered with a light litter layer	grndns ²

¹Names are acronyms used by the HSI software, except 'grndns' and 'grndfd.'

²Variables not in the HSI model (Schroeder 1985).

³Densities were estimated for each of 6 size classes (≥ 25.4 , ≥ 27.9 , ≥ 30.5 , ≥ 33.0 , ≥ 35.6 , and ≥ 38.1).

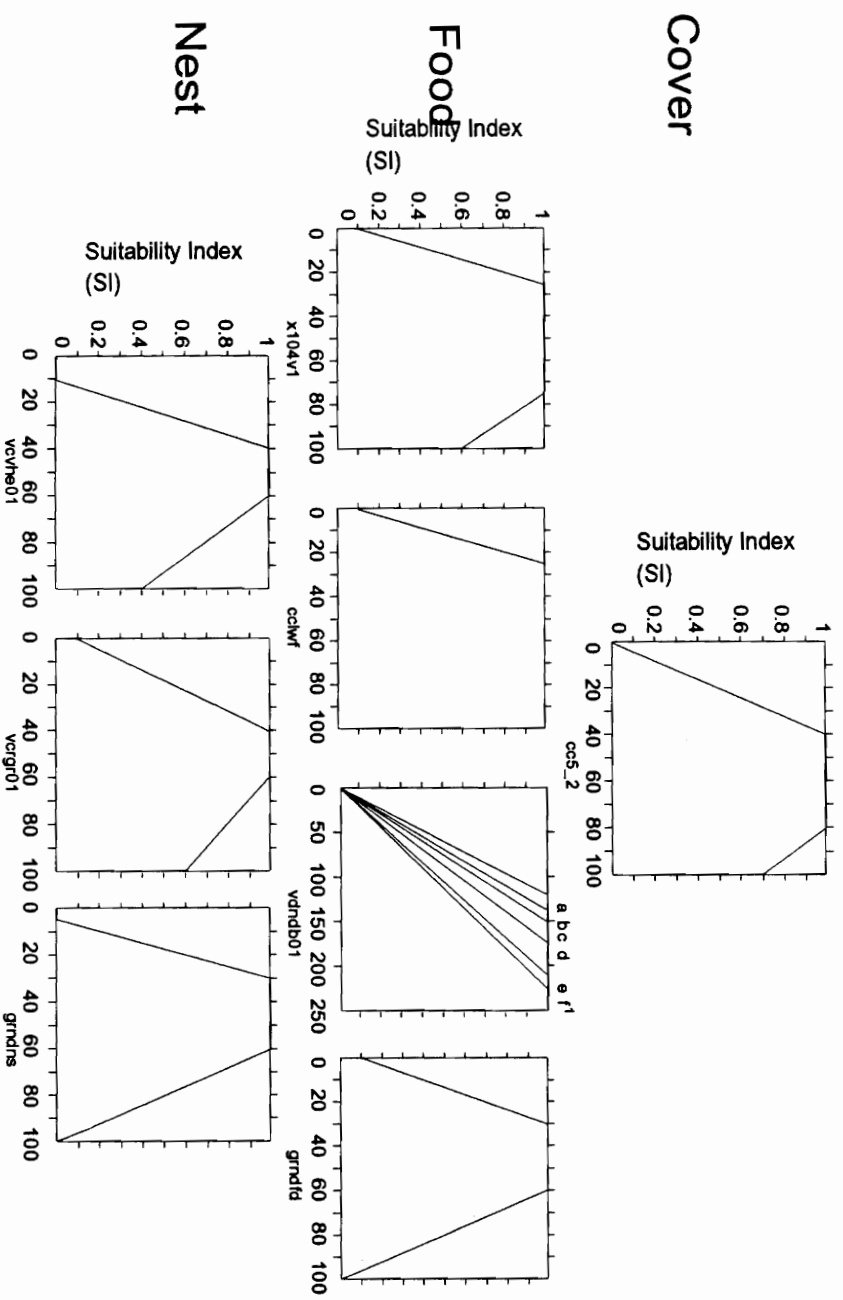
⁴Canopy cover of woody vegetation < 2 m high was used as an approximation.

ground-level vegetation is very critical (Rice et al. 1993). Bobwhites cannot feed in thick mats of vegetation (Schroeder 1985). Stoddard (1931) recognized ideal foraging conditions as areas with open vegetation interspersed with some bare ground. Ease of movement at ground level and more importantly, access to seeds, are critical to the bobwhite and both are determined by the extent of bare or lightly-littered ground. The percent bare or lightly-littered ground is the final of 4 variables used to evaluate the winter food potential of a site (Table 1, Fig. 2).

Cover Life Requisite. — Although it is adapted to a wide range of conditions, the bobwhite's distribution throughout most of its range has been shown to be associated with the availability of dense escape cover. That Roseberry and Klimstra (1984) identified low, dense, woody cover as 1 of the 4 essential components of bobwhite habitat is consistent with earlier, as well as later accounts describing the cover needs of the bobwhite. This type of vegetation, i.e., dense, shrubby growth, has been appropriately described as escape and/or foul weather cover (Davis 1964). These areas of rank, woody growth, typically 1-3 patches per covey winter range, are used extensively during midday and provide protection from diurnal predators (Schroeder 1985). Rosene (1969) noted that dense thickets of low brush were frequently used as a means of avoiding predators. A single variable, the percent canopy cover of

Life
Requisite

Suitability Indices



¹Curve used is a function of the mean dbh of trees > 25.4 cm. See Table 1 for size classes corresponding to each letter.

Figure 2. Suitability Indices (SI) for 8 variables composing the CRP HSI model for the northern bobwhite.

woody vegetation 0.5-2 m, is used in the model to assess a site's ability to provide cover for the bobwhite. The density of woody vegetation < 2 m was used as an approximation for this variable (Table 1, Fig. 2).

Nest/brood Habitat Life Requisite. — A wide range of habitats are used by nesting bobwhites. Pastures, broomsedge (*Andropogon virginicus*) fields, hayfields, fencerows, and weedy roadsides have been identified as suitable nesting habitat (Parmalee 1953, Dimmick 1968, Roseberry and Klimstra 1984). However, habitats characterized by scattered shrubs and brambles with a moderate stand of herbaceous and grassy vegetation, variously described as old-fields, fallow fields, and idle fields, are the most typical sites used by nesting bobwhites (Roseberry and Klimstra 1984). Clumped vegetation, preferably grasses, and the absence of a dense sod, which prohibits movements by hens and chicks, provide ideal nesting conditions (Bidwell et al. 1991). The CRP HSI model uses estimates of canopy cover of herbaceous vegetation, the percent of the herbaceous canopy that is grass, and the amount of bare or lightly-littered ground as indices of nest habitat suitability (Table 1, Fig. 2).

Life Requisite Suitability Indices

Winter Food Life Requisite. — Model developers assumed that grain crop residues alone are capable of supporting maximum numbers of bobwhites (Schroeder 1985). However, it is believed that neither herbaceous foodstuffs nor hard mast are of comparable quality as crop residues and thus, only when the former 2 are combined, does the potential for maximum numbers of quail in forested, shrub, and herbaceous cover types exist. Further, it is assumed that herbaceous quail foods are twice as important as mast. Thus, for non-crop habitats that do not provide mast, the Life Requisite Suitability Index (LRSI) for winter food is estimated as follows:

$$\text{LRSI}_2 = 2/3 * (\text{SIV}_2 * \text{SIV}_3)$$

For those habitats capable of providing pine/oak mast, the LRSI for winter food is determined as follows:

$$\text{LRSI}_3 = \text{LRSI}_2 + 1/3 * (\text{SIV}_4)$$

Finally, for cropfields and a group of early-successional habitats the LRSI for winter food is equal to

$$\text{LRSI}_1 = \text{SIV}_2$$

Cover Life Requisite. — The density of woody vegetation <2 m high is assumed to be an adequate measure of the ability of a site to provide protective cover. As a

result, the LRSI for cover is equal to SIV5 (Table 1, Fig. 2).

Nest/brood Habitat Life Requisite. — The 3 variables representing the nest/brood habitat life requisite (Table 1, Fig. 2) are weighted equally and combined as follows to yield the LRSI for nest/brood habitat:

$$\text{LRSI} = (\text{SIV6} * \text{SIV7} * \text{SIV8})^{1/2}$$

Equivalent Percent and Composition Suitability Indices

Although no single cover type within an area is likely to provide all 3 life requisites, it is unlikely that several cover types on any given evaluation site may have an LRSI value >0 for a given life requisite. As a result, an additional model component was needed to accommodate variations in size among cover types. Model developers addressed this by explicitly assuming that a compensatory relationship exists between the quantity and quality of a resource. For example, 100 ha of land with a winter food LRSI of 0.5 is assumed to have the same potential to support a population of quail as 50 ha rated at a LRSI of 1.0, all other factors being equal. This estimate of habitat suitability is operationally defined as the product of the relative (% of evaluation site) area of the each type and the associated LRSI.

Summed over all contributing habitats, this value represents the "equivalent" percent of the evaluation site providing the life requisite in optimum condition.

Model output for multiple cover type models such as the northern bobwhite HSI is a function of the life requisite assumed to be most limiting. However, to make this determination an additional set of SI curves are required. These curves, 1 for each life requisite, represent hypothesized relationships between habitat quality and the equivalent percent of the evaluation site providing the life requisite in optimum condition. The implicit assumption underlying these curves, which are labeled Composition LRSI, is that an optimum combination of life requisites in optimum condition exists and that deviations from this combination result in lower quality habitat.

Quail habitat quality is a function of winter food, cover, and nest/brood habitat and exists only when all 3 occur together. Based on a synthesis of previous work (Edminster 1954, Rosene 1969), Schroeder assumed that ideal habitat conditions exist when the equivalent percent of the area providing optimum winter food, cover, and nest/brood habitat is 80, 20, 10%, respectively (Fig. 3).

METHODS

All models, including the HSI model for the northern bobwhite, are attempts

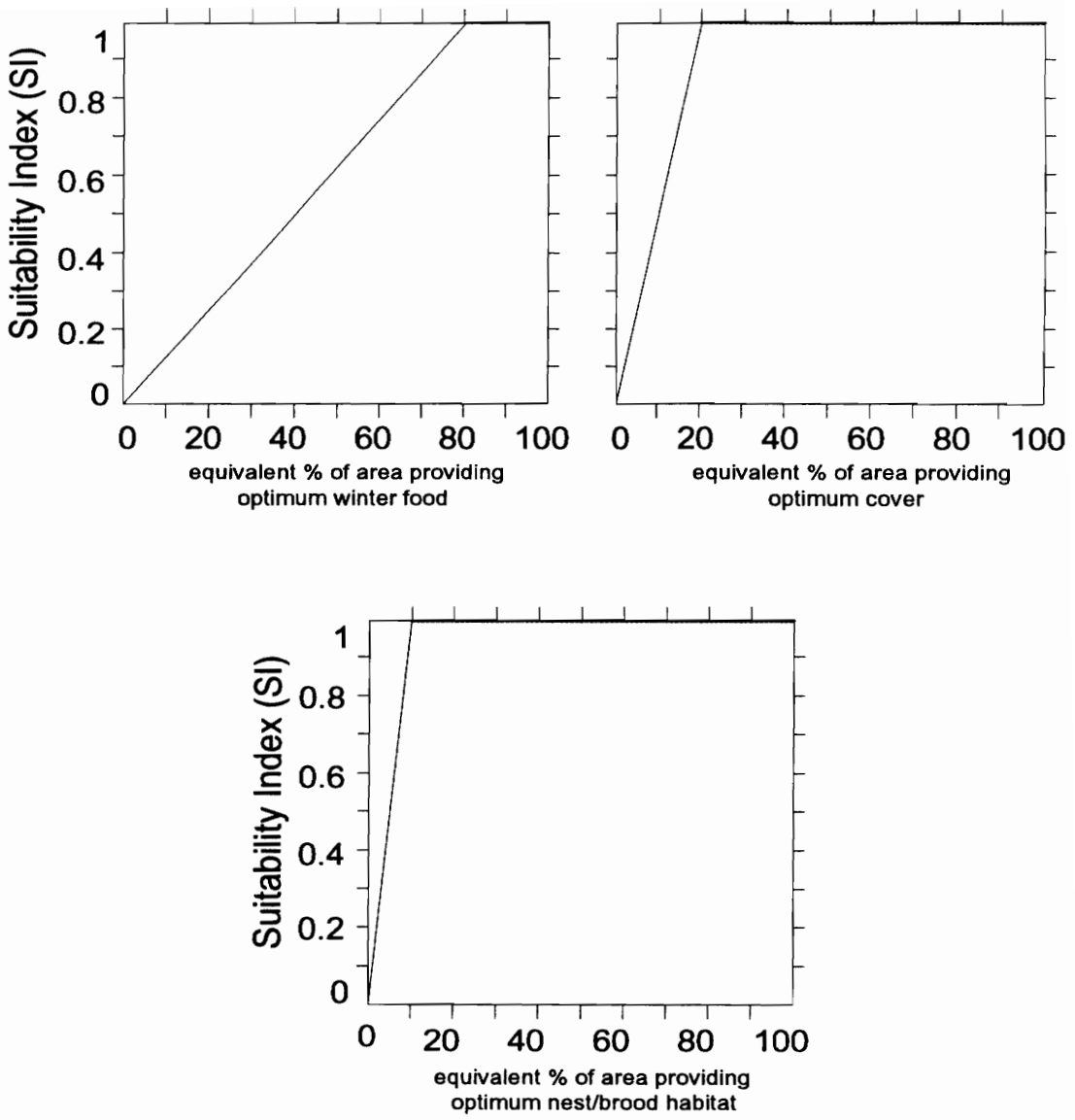


Figure 3. Suitability indices for equivalent percent of area providing winter food, cover, and nest life requisites in optimum condition. Curves are reproduced from Schroder (1985).

to mimic reality. The extent to which they succeed can only be determined by comparing their output with some measure of reality. The HSI model for the northern bobwhite is presumed to be a model of the processes that determine the upper limit of population performance at any given site, i.e., carrying capacity. I assumed that spring call count data also were such an index. To the extent that these assumptions are true, it is hypothesized that a positive correlation exists between HSI model output and the number of whistling males detected across the evaluation sites examined in this study.

Study Site Selection

The present investigation began in 1986 as an effort to document the relationship between agricultural land use patterns and northern bobwhite population levels (Cline 1988). Consequently, an attempt was made to select study sites that represented a continuum of major land use combinations for this region, from sites that were dominated by a single cover type to sites where nearly all cover types were represented. Sizes and shapes of cover type patches and juxtaposition with other cover types were features considered as well in an attempt to adequately represent the study area. Because roadside counts were to be used to estimate relative bobwhite population levels, potential sampling sites were limited to primary county

roads.

Black and white aerial photos of the county were used to identify potential sampling locations. Roads within 800 m of a previously selected road were excluded from consideration to avoid double sampling. Ten roads, hereafter referred to as transects, were selected for sampling. This number represented a compromise between the time needed to adequately collect both spring whistle count and land use data from each site, and our primary objective of maximizing the diversity of land use types sampled.

Spring Call Counts

It is believed that the maximum detection distance for a calling male is approximately 400 m (Rosene 1969). Consequently, listening stops along each of the transects were placed 800 m apart, for a total of 121 stops, hereafter referred to as stations. The number of stations on each transect ranged from 10-13.

Counts were begun approximately 0.5 hr before sunrise on days when precipitation did not exceed a drizzle and winds were < 10 km/hr. Count duration at each station was 10 min, during which time we attempted to count, only once, all individual whistling males (Rosene 1969). To reduce the likelihood of double counting, the station was divided into quarters and calls were recorded by quarter.

Counts generally lasted approximately 2 - 2.5 hr. Transects were sampled sequentially and the order of sampling along each transect was reversed on subsequent visits to avoid temporal biases that might be associated with sampling stations at a given time.

Data collected during the first 3 visits to each station were not used to generate station means, except for 1986. Means for these first runs for all years, although not statistically compared, were considerably lower than subsequent runs and thus it was assumed that calling activity was well below peak levels during the first 3 runs. Because censusing was conducted nearly into August during 1986, well after the peak of calling, which occurs in mid-June in most of the Commonwealth (Fies pers. comm.), call count data gathered during the first 2 and the final visit to the 121 stations in 1986 were not used (Fig. 4). The pattern observed in the 1986 calling data was used to determine the sampling time frame in subsequent years. However, the need to devote field time to other tasks resulted in a truncated sampling period for years 1987-91. Variability in the number of visits notwithstanding, as long as all stations are equally affected or unaffected by events that might influence calling activity, I assumed the data sets should be comparable. The mean number of birds detected per visit was estimated for each station for each of the 6 sampling years. I then averaged annual means for a grand mean for each

Quail Detected per Visit

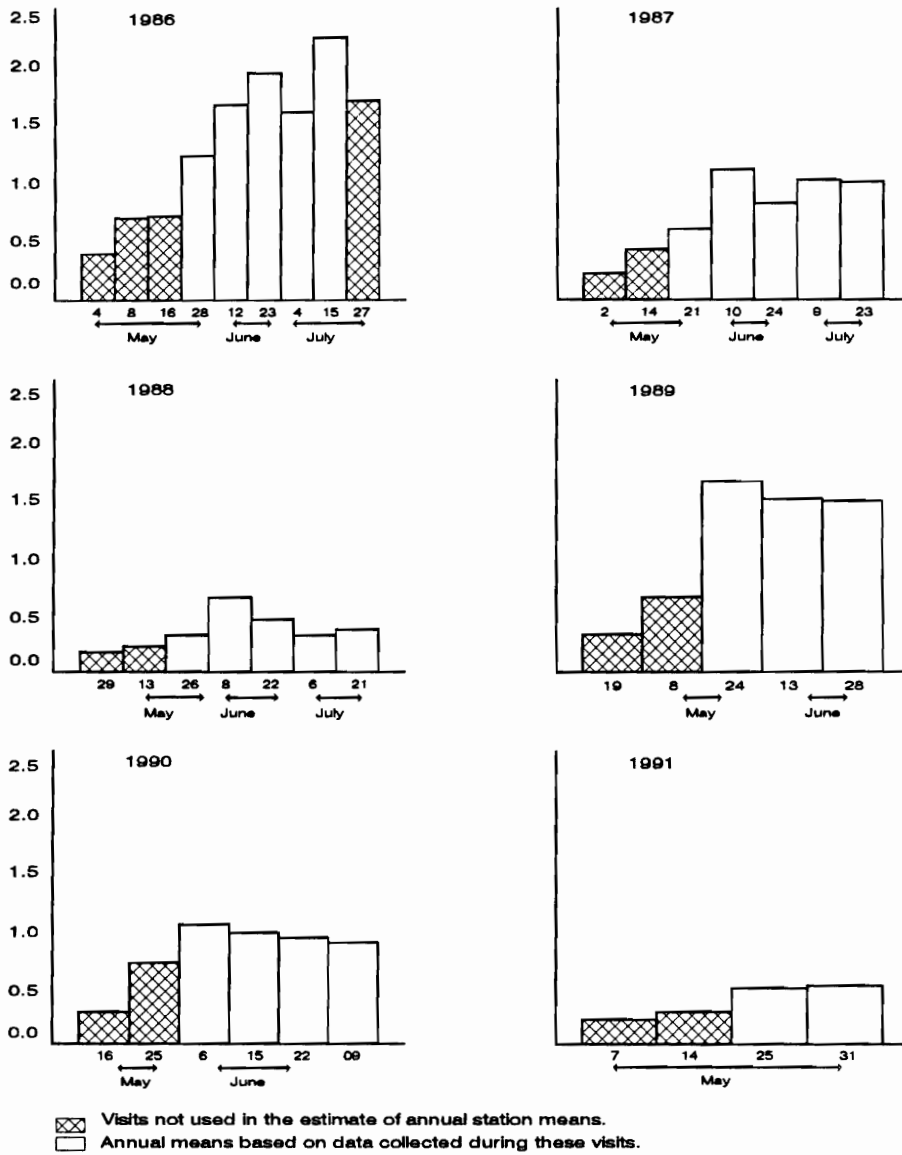


Figure 4. Mean number of quail detected per visit per station. Means are based on 121 stations across 10 transects sampled 1986-1991, Halifax County, Virginia. Early and late visits were excluded because of potential temporal biases associated with calling activity.

station. The resulting value provides an estimate of the number of birds detected per visit per year.

Habitat Sampling

The HSI model for the northern bobwhite is a multi-cover type model. Because the primary unit of analysis is the cover type, the development of a cover type map of the evaluation site is a necessary first step in the application of the model. Subsequently, values for the 8 variables representing the 3 life requisites must be estimated for all appropriate cover types.

Cover type map development began with the delineation of each station and major cover type boundaries on aerial photos. I initially recognized 6 major cover types (crop, pasture, pond, residential, road, and forest). These were selected because they were generally discernable from 1:660 black and white aerial photographs. Each of approximately 3,500 individual cover type polygons collectively representing the 121 stations were ground-truthed to verify boundaries and in the case of forests, pastures, and crops, to further classify the cover type. Forested cover types were reclassified according to stocking rates (light, medium, or heavy) in each of 3 tree size classes: sapling <3 cm dbh; pole 3-25 cm dbh; and saw timber \geq 25 cm dbh. Pastures were classified as either typical grassland/hayland or grazed woodlands. The latter were further classified in a manner similar to the

forested habitats. Finally, crop fields were classified as active, fallow, or fallow with saplings. Each polygon received 1 of 28 cover type classifications (Table 2). Ground-truthing was completed during the summer of 1986. Cover type maps were updated annually. Although I did not annually systematically survey each of the approximately 3,500 polygons for boundary or cover type changes, I believe that few, if any, changes went unnoticed because of the time spent on the ground checking crop fields for changes. Although annual updates of the cover maps were completed by various personnel, the original maps were developed by a single observer and an assistant. Consequently, I assumed that, except for random variation, there was little observer bias in the cover type maps.

Because it would have been logistically impossible to evaluate conditions in all 3,500 polygons representing the 121 stations, a random sample of each cover type was used to estimate mean SI values for all 8 model variables (Table 1). These means were subsequently used for all occurrences of the respective cover type.

To facilitate vegetation sampling, I developed a 121x28 matrix of stations by cover types. For each cover type, I randomly selected 25 stations for sampling. I then used the cover maps for each station to determine if the cover type was present at each of the stations selected. In those instances where ≥ 1 polygon was present, I randomly selected from those available. When the cover type was absent, I selected

Table 2. Mean patch size (ha), mean percent composition at each station (n=121) and correlation of percent composition at each station with the quail index for 28 cover types sampled, 1986-1991, Halifax County, Virginia.

Habitat	Patch Size (ha)			%Composition (n = 121 stations)			Correlation (n = 121 stations)	
	n	\bar{X}	SE	\bar{X}	SE	r	P	
Woodlands^a								
LOW CANOPY WOODLANDS								
Saplings, light	28	0.37	0.07	0.17	0.05	0.11	0.22	
Cutover with Saplings, light stocking	11	1.52	0.91	0.30	0.18	0.01	0.93	
Saplings, heavy stocking	36	0.62	0.16	0.45	0.12	-0.06	0.5	
Saplings, heavy stocking; Poles, light stocking	123	1.48	0.25	3.11	0.61	-0.01	0.92	
Cutover with Saplings, medium stocking; Poles, light	72	2.64	0.42	3.22	0.70	0.06	0.48	
Low Canopy Woodlands	270	1.60	0.17	7.25	0.92	0.08	0.40	
MEDIUM CANOPY WOODLANDS								
Saplings, light stocking ; Poles, medium stocking	216	0.79	0.07	2.93	0.42	0.04	0.69	
Poles, medium stocking	63	0.60	0.20	0.64	0.23	-0.03	0.74	
Saplings and Poles, medium stocking	151	1.06	0.13	2.71	0.42	-0.16	0.07	
Medium Canopy Woodlands	430	0.86	0.07	6.29	0.62	-0.10	0.30	
HIGH CANOPY WOODLANDS								
Saplings, Pole and Mature, light stocking	411	2.25	0.15	16.06	1.48	-0.32	0.001	
Pole and Mature, light stocking	87	0.94	0.13	1.4	0.31	0.00	1.0	
Saplings and Pole, medium stocking; Mature light	381	3.12	0.21	20.28	1.65	-0.17	0.06	

Table 2. Continued.

Habitat	Patch size (ha)			%Composition (n = 121 stations)			Correlation (n = 121 stations)		
	n	\bar{X}	SE	\bar{X}	SE	P	r	P	
Saplings, heavy stocking; Pole and Mature, light	76	1.61	0.37	2.09	0.58		-0.04	0.62	
High Canopy Woodlands	955	2.43	0.11	39.8	1.69		-0.46	0.001	
Grazed Woodlands									
Saplings, Pole and Mature, light stocking	14	2.34	0.54	0.54	0.19		0.19	0.03	
Pole and Mature, light stocking	11	0.80	0.28	0.15	0.07		0.10	0.30	
Saplings and Poles, medium stocking; Mature, light	6	3.63	1.25	0.39	0.20		0.06	0.51	
Saplings, heavy stocking; Pole and Mature, light	5	1.78	1.21	0.16	0.13		-0.03	0.78	
Saplings, light stocking	12	1.16	0.45	0.24	0.09		0.09	0.31	
Cutover with Saplings, light stocking	1	6.65	.	0.11	.		-0.02	0.79	
Saplings, light stocking; Poles medium stocking	7	1.59	0.81	0.19	0.12		0.11	0.25	
Cutover with Saplings, medium stocking; Poles, light	7	0.81	0.66	0.09	0.09		0.00	1.0	
Cutover with Saplings, medium stocking; Poles and Mature, light stocking	1	2.46	.	0.04	.		-0.07	0.47	
Saplings, heavy stocking	2	0.31	0.01	0.01	0.01		-0.04	0.64	
Poles, medium stocking	6	0.72	0.39	0.07	0.07		0.03	0.76	
Saplings and Poles, medium stocking	1	1.08	.	0.02	.		-0.1	0.28	

Table 2. Continued.

Habitat	Patch Size (ha)			%Composition (n = 121 stations)			Correlation (n = 121 stations)
	n	\bar{X}	SE	\bar{X}	SE	r	
Other Habitats							
Crop	635	0.77	0.04	8.4	0.77	0.24	0.01
Pasture/hayland	425	2.01	0.13	14.4	1.68	0.28	0.001
Fallow field	620	0.80	0.04	8.5	0.60	0.16	0.07
Fallow with saplings	81	0.86	0.10	1.21	0.17	0.03	0.76

Woodlands were classified according to composition (saplings < 3cm dbh; 3 ≤ poles < 25 cm dbh; mature > 25 cm dbh) and relative stocking rates (light < 25%; 25 ≤ medium < 50; and heavy > 50 % coverage) in each size class. Stocking rates are an "ocular" estimate of % coverage.

an alternate station. I identified all landmarks that either were adjacent to (e.g., corners) or in close proximity of the cover type to be sampled. One landmark was randomly selected and noted on the cover map. Once in the field, I located the landmark and traveled a random distance (0-50 m) along a randomly selected azimuth to the vegetation transect starting point. The sampling transect continued along this same vector. An alternate vector was used in those instances where sampling took me out of the cover type.

Means for all parameters except the density of mast trees/ha were estimated during the spring and summer of 1991. The HSI model specifies that these measurements be made during these seasons. However, because tree density was not a function of season, these data were collected during late-winter and early-spring of 1991. Means for the percent canopy cover of herbaceous quail foods, late-winter quail foods, woody vegetation < 2 m, herbaceous vegetation, and percent of herbaceous canopy that is grass, as well as the percent bare or lightly-littered ground, were based on point sampling (Hays et al. 1981) at 1 m intervals along a single 50 m transect traversing the cover type polygon. Coverage estimates were based on the number of "hits" out of a possible 50. A hit occurred when vegetation intersected a 3/8" dowel placed vertically at each sampling point. If a litter layer or bare ground was plainly visible at the sampling point, the ground was considered

bare at that site. The density of mast trees > 25.4 cm dbh/ha was determined in 2, 0.04 ha circular plots randomly located within the cover type to be sampled. Trees > 25.4 cm dbh were placed in 1 of the 6 dbh classes (Table 1). To estimate the average dbh of the plot and subsequently the stand, I calculated a weighted mean dbh based on the midpoints of each dbh category.

After an initial round of sampling, I adjusted sampling effort based on observed variation within each of the cover types. Homogeneous habitat types such as mature woodlands and pastures were sampled at a lower rate than many of the early-successional habitats because of the large degree of variation in the parameters being estimated in these later cover types.

HSI Value Determination

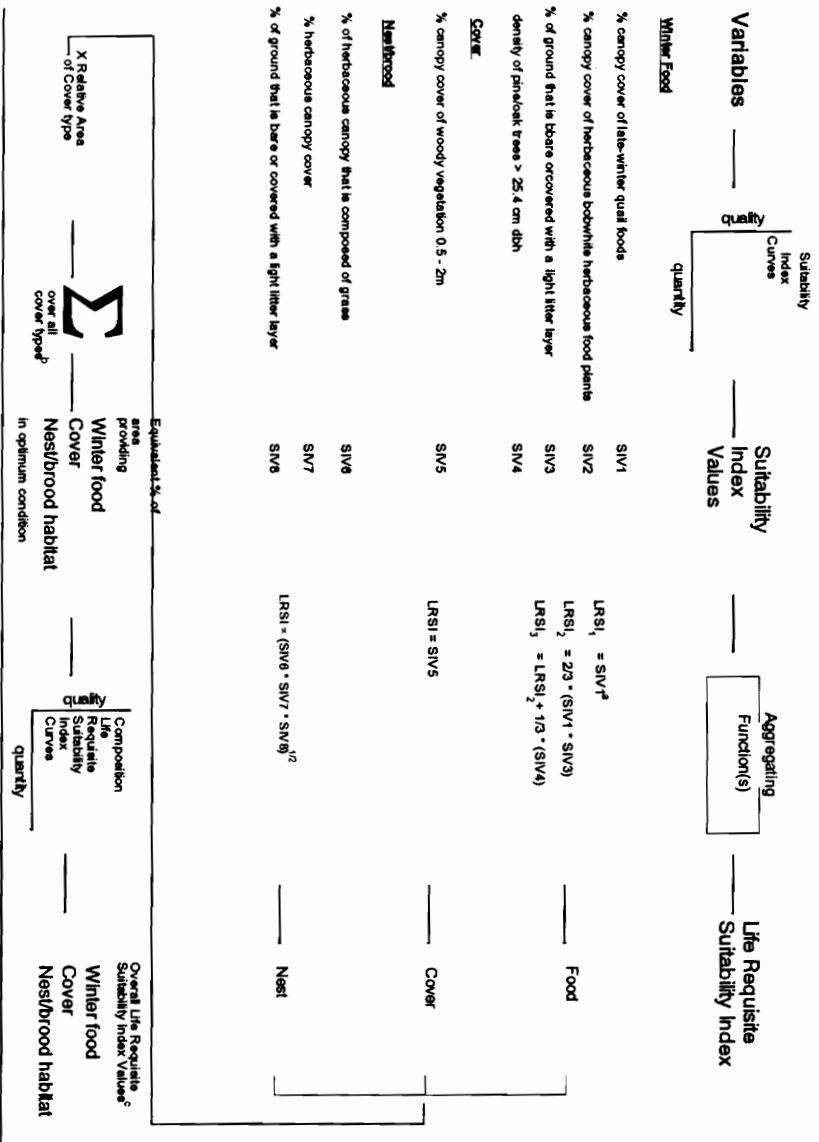
Because the hypothesized relationships between habitat conditions and suitability in Figure 2 are non-linear, I converted vegetation measures to SIs before computing a mean SI for each variable for each cover type. I then computed Life Requisite Suitability Indices (LRSIs) for each cover type and merged these values with the polygon attribute data. This data set included cover type and relative (% of the entire station) area estimates for each of the approximately 21,000 (3,500x 6 years) polygons. Equivalent percent of the station providing each life requisite in

optimum condition was estimated by multiplying the relative area of each polygon by the appropriate LRSI and then summing over all appropriate polygons. These values were computed for each of the 6 years of the study and averaged for a grand mean. Finally, composition Suitability Indices (SIs) were estimated according to the curves in Figure 3. Model output was equal to the smallest of these 3 SIs. All computations were performed using SAS (1985). Figure 5 summarizes the computation of the HSI score.

Model Performance

To the extent that the number of calling males is an index of potential population performance, one would expect a positive relationship between this index and HSI model output, assuming that the latter is also an index of potential population performance. I evaluated the validity of these deductions by calculating a Spearman's rank correlation between these 2 indices. A nonparametric test was used because the data were not normally distributed.

Each of the SI curves composing the northern bobwhite HSI model are assumed to represent an upper limit to population performance given the habitat conditions present. These estimates of potential performance are expressed as a percent of the theoretical maximum performance possible under any conditions



*LRSI used is a function of the habitat type being evaluated. See text.
 Summation is over all occurrences of all appropriate cover types within the area being evaluated.
 Model outputs equal to the smallest of the three Overall LRSI values.

Figure 5. Summary of steps involved in the computation of Habitat Suitability Index (HSI) values for 121 stations sampled 1986-1991, Halifax County, Virginia.

within the range of model applicability. Thus, in evaluating HSI models, it is not sufficient that model output simply be correlated with the performance measure, it is also necessary to determine if in fact the SI curves do represent an upper limit to population performance. This determination was made by expressing the index of abundance at each station as a percent of the maximum number of birds recorded on the study area and comparing these values with the corresponding estimates of potential population performance, i.e., model output. Expressing population performance at each of the 121 stations as a percent of 2.72, rather than the maximum value in Table 3, and adjusting the draft model to fit the data, should yield a model applicable for the entire piedmont physiographic region of Virginia and North Carolina.

RESULTS AND DISCUSSION

Spring Call Counts

The mean number of quail detected on the study area varied considerably over the course of the 6-year study (Multiple Response Permutation Procedure [MRPP] $\delta = 0.33$, $P < 0.001$, Table 4). The greatest number of birds were detected in 1986 and the least in 1988 ($P < 0.01$). The trend in the call count data observed during the first 3 years of the study was repeated during the last 3 years.

Table 3. Northern bobwhite spring whistle call count data for various locations from the Midwest and Southeast portions of the species' range.

Location	Date	Source	Abundance index	Methods ^a
Jasper County, South Carolina	1983	Breck Carmichael, South Carolina Wildlife and Marine Resources Department	11 calling males/stop	Index based on 12 stops spaced at 0.5 mile intervals. Routes were sampled between 15 June and 10 July. Counts began at official sunrise. Count duration was 8 min. per stop.
Virginia Beach County, Virginia	1990	Mike Fies, Virginia Department of Game and Inland Fisheries	10.5 calling males/stop	Index based on 10 stops spaced at 1 mile intervals. Routes sampled during mid-July. Counts were conducted during "calm," mild weather. Counts began at official sunrise. Count duration was 2 min. per stop.
Kansas, Cropland Study Area	1994	Scott Taylor, Department of Wildlife Ecology, University of Wisconsin	5.8 calling males/stop	
Southern Mississippi, Overgrazed pasture/woodlands intensively managed for quail	1991	Wes Burger, University of Mississippi	6.0 calling males/stop	
Kosciusk County, Indiana	1957	Brian Frawley, Indiana Department of Natural Resources	10.5 calling males/stop	
Western Illinois	1968	Preno, W.L. and R.E. Labisky, 1971. Abundance and harvest of doves, pheasants, bobwhites and cottontails in Illinois, 1956-1969. Ill. Dept. Cons., Tech. Bull. No. 4. 76pp	5.25 calling males/stop	

Table 3. Continued.

Location	Date	Source	Abundance index	Methods
Ames Plantation, Western Tennessee	1973	Saunders, R. H. 1973. Some behavioral and demographic characteristics of a bobwhite quail population. M.S. Thesis, Univ. of Tenn., 83pp.	6.75 calling males/visit	Index based on 3 sites, each visited 16 times between 10 May and 24 August.
Fort Bragg Military Base, Fort Bragg, North Carolina	1986	Phil Doerr, North Carolina State University	4.1 calling males/stop	
Piedmont Physiographic Region, North Carolina	1957-1974	Terry Sharpe, North Carolina Wildlife Resources Commission	2.73 calling males/stop	Mean is based on data collected from 17 routes throughout the Piedmont region of North Carolina.
Halifax County, Virginia	1986-1991	Present study	1.0 calling males/stop	Index is based on ≥ 4 visits/year to 121 sites distributed along 10 transects. Total stops /transect ranged from 10-13.

^a Although methods are presented for a selected few of the sources, spring whistle count surveys are generally standardized, varying only slightly from region to region, typically only in count duration. Effects of weather and interval distance are most critical and usually given the greatest consideration.

Table 4. Mean number of quail detected per transect per visit and representation (% of total station area) of 5 general land use types for 10 transects sampled 1986-1991, Halifax County, Virginia.

Crop	Year															P ^c			
	1986			1987			1988			1989			1990				1991		
	X	SE		X	SE		X	SE		X	SE		X	SE			X ^a	SE	MRPP ^b
quail/ transect/ visit	1.67a	0.15		0.94b	0.09		0.42c	0.04		1.54a	0.14		0.90b	0.06		0.48c	0.06	-14.6	<0.001
cropland	19.7a	2.18		19.2a	2.14		19.6a	2.21		17.6a	2.23		17.5a	2.16		18.1a	2.27	1.9	1.0
pasture/ hayland	14.9a	3.10		14.3a	2.96		14.4a	2.92		15.8a	2.94		14.9a	2.76		13.3a	2.88	2.19	1.0
low canopy woodlands	6.9a	0.98		7.4a	0.91		7.8a	1.13		7.5a	0.83		7.9a	0.77		9.2a	1.06	1.46	0.97
medium canopy woodlands	6.7a	0.98		6.6a	0.99		6.7a	0.94		6.6a	0.95		6.5a	1.0		6.5a	0.99	2.27	1.0
high canopy woodlands	42.6a	2.53		42.2a	2.06		41.3a	1.89		41.6a	2.02		41.6a	2.05		41.5a	2.33	2.43	1.0

^aMeans within a row not sharing a common letter are different ($P < 0.01$). Pairwise comparisons were performed using Multiple Response

Permutations Procedures running on Blossom Statistical Software (1992). Sample size for all comparisons was 60.

^bStandardized test statistic for MRPP test.

^cProbability that ≥ 2 of the means were different.

From 1986 levels, quail numbers declined steadily for 2 years and then returned to levels observed in 1986. Quail numbers subsequently declined again during 1990 and 1991. Population levels during each "3-year cycle" were similar. Call count data from the Piedmont physiographic region of North Carolina showed a similar trend, with the only difference being that the upward trend in their population lasted a year longer than the present study (Fig. 6). Trends in call count data from Halifax County collected by the Virginia Department of Game and Inland Fisheries (VDGIF) were not entirely consistent with data from either the present study or the North Carolina data. A notable difference was 1986 estimates (Fig. 6). Of the 6 years of call count data collected, the greatest number of quail detected on my study area occurred in 1986. Data from VDGIF were exactly opposite, with 1986 levels < all other 5 (1987-1991) years (Fig. 6).

Annual fluctuations in northern bobwhite populations are often closely associated with weather conditions, which can have a marked effect both during the nesting and brood rearing seasons, as well as the winter months (Roseberry and Klimstra 1985, Edminster 1954). It is likely that weather is at least partly responsible for the trends observed in the present study. Land use changes may have contributed as well.

Much of the southeastern U. S. experienced a drought during the spring and

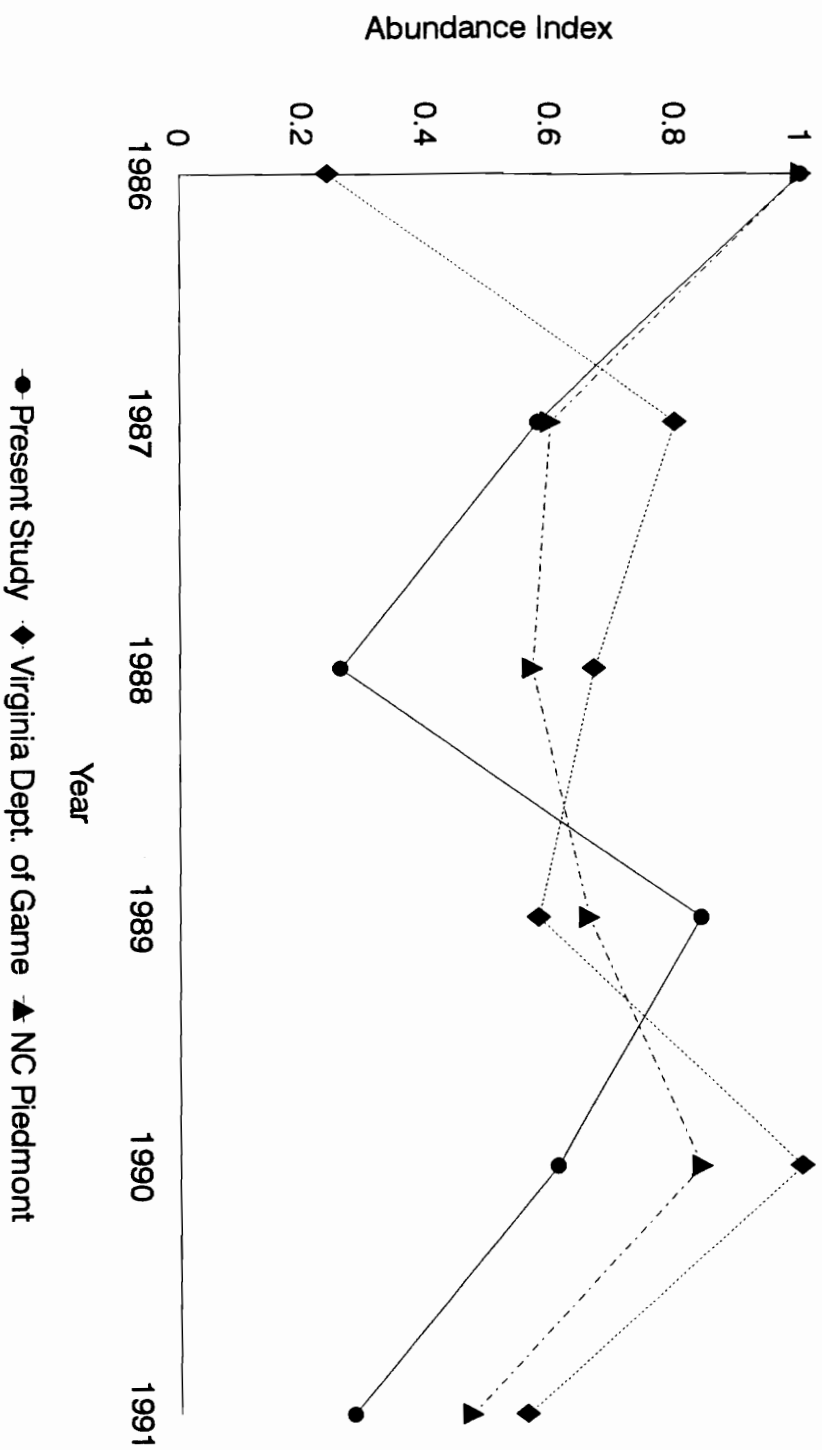


Figure 6. Comparison of population trend data for the present study with indices of abundance based on call count data from Virginia Department of Game and Inland Fisheries (VDGIF) and the Piedmont Physiographic region of North Carolina. Data from VDGIF were collected mid-July during a single visit to 30 stops along three transects throughout Halifax County. Data from North Carolina were collected over a similar period. The original abundance index, number of quail detected per visit or number of calls per stop, was scaled to 1 for comparative purposes.

summer of 1986 (Cline 1988). This shortage of rain likely reduced quail populations via reduced reproductive output (Rosene 1969). Numerous factors including decreased intake of macronutrients such as phosphorus, nonspecific stress response, and reduced food intake and subsequent nutrient intake have been proposed as potential contributors to reproductive failure associated with water shortage in south Texas (Koerth and Guthery 1991). These authors observed an absence of ovary and oviduct development in water-stressed female bobwhites. Earlier workers noted that an increase in nest abandonment, a reduction in the hatchability of eggs, and a reduced food supply were typical during the nesting and brood rearing seasons of drought years (Stoddard 1931, Murray 1958, Reid and Goodrum 1960). Decreased population index levels in 1987 were likely a direct result of the drought conditions. Because 1987 was relatively normal in terms of precipitation and temperature (Table 5), it is unlikely that the continued decline in the population levels observed in 1988 was due entirely to the same events that resulted in 1987 population levels. However, a lag effect may have contributed to the decline.

Roseberry and Klimstra (1984) demonstrated a relationship between snow cover and recruitment the subsequent summer. They showed that the number of days of snow cover > 2.54 cm was related negatively to the rate of population gain

Table 5. Precipitation (cm) and mean monthly temperature (C°) data for Halifax County, Virginia, 1985-1991. Data were recorded at South Boston, Halifax County, Virginia.

Year	Month ^a												
	April			May			June			July			
	Rainfall (cm)	Deviation from normal ^b	Temp. (C°)	Rainfall (cm)	Deviation from normal	Temp. (C°)	Rainfall (cm)	Deviation from normal	Temp. (C°)	Rainfall (cm)	Deviation from normal	Temp. (C°)	
85	3.0		15.6	22.6		19.1	15.5		22.4		33.3		24.7
86	3.0	-2.34^c	14.3	25.9	-1.16	18.2	3.3	-2.7	23.9		26.7	-0.82	26.7
87	37.3	5.34	10.8	15.2	-1.71	18.9	16.3	-0.21	23.4		21.6	-0.42	26.0
88	22.6	-0.16	11.2	11.7	0.03	16.1	33.5	-1.12	20.8		48.3	1.63	24.1
89	33.0	0.57	12.4	23.1	2.74	16.3	53.8	4.28	24.3		42.4	4.52	25.8
90	27.7		13.3	38.9		17.3	21.1		22.4		22.9		25.7
91	20.3	-0.59	14.2	12.4	0.96	20.2	20.8	-0.68	23.8		18.3	2.16	24.6

^aSource: Climatological Data for Virginia, NOAA, Volumes 95-101:4-7.

^bSince long-term data were unavailable for South Boston, data for the Climatological Division that South Boston is a part of, were used as an approximation.

^cMost of Southeastern U.S. experienced a drought in 1986.

of quail in Illinois. Snow cover is believed to prohibit and/or reduce the bird's ability to forage for shed seeds. Weather conditions during the winter of 1987 may have sustained the decline that began in 1986. There was an unusually high number of days of snow cover (Table 6), both trace and days when snow depth > 2.54 cm during January, February, and March of 1987. Snow cover in January exceeded 25.4 cm 8 of 11 days where snow depth > 2.54 cm was reported. Beyond these weather events, i.e., the drought of 1986 and the winter of 1987, it is difficult to determine what role if any weather played in the increase in population levels observed in 1989 and the subsequent decline.

A general pattern that I observed for many of the crop fields in Halifax County was to plant winter wheat after harvesting tobacco in the fall and then to plant either soybeans or leave the field idle after harvesting the wheat in the spring. In either case, the field would have wheat or bean stubble the following winter and presumably more food available than if the field had been fall plowed after harvesting the tobacco. Because of positive correlation ($r_s = 0.29$, $P = 0.001$, $n=121$) between the area of each station planted to wheat and the number of males detected, it seemed reasonable to consider the possibility that the dynamic nature of land use, specifically the rotation of crops, may have had some role in influencing the patterns observed in quail population levels over the course of the study.

Table 6. Snow-cover days data for Lynchburg regional airport, Cambell County, Virginia, 1985-1990. Data are used as an approximation for conditions in Halifax County, which borders Cambell County to the south. of the airport^a.

Year	Month					
	January		Feburary		March	
	> 2.54 cm	Trace	> 2.54 cm	Trace	> 2.54 cm	Trace
1985	1	9	0	0	0	1
1986	1	5	4	2	0	0
1987	11 ^b	0	11 ^c	9	1	2
1988	12	2	-	-	-	-
1989	1	0	5	5	0	2
1990	0	1	0	1	1	1

^aSource: Climatological Data for Virginia, NOAA, 95-101:4-7.

^bSnow cover was > 25.4 cm for 8 days.

^cSnow cover was > 12.7 cm for 6 days.

MRPP tests revealed no ($P > 0.05$) differences in the relative proportions the 5 primary land use types on the study area over the 6-year study period (Table 4). However, the amount of corn ($P < 0.001$, MRPP $\delta = 8308.8$), grain/hay ($P < 0.001$, MRPP $\delta = 606.6$) and unknown crop types ($P < 0.01$, MRPP $\delta = 162.8$) grown on the study area differed among the 6 years for which call count and land use data were collected (Table 7). However, there was no apparent relationship between cover of these crop types and the count index (Table 3). It is likely that weather related events were responsible for the declines in 1987 and 1988 population levels. However, it is uncertain what role weather and changing land use may have had in the trend observed in the population from 1989-91.

Habitat Sampling

Forested habitats represented, on average, 53% of the area at any given station (Table 2). Most of this area (68%) was composed of multilayered forests, particularly those with light stocking in all layers and forests with medium-stocked sapling and pole components and lightly-stocked saw timber. Cropland, including fallow land, represented on average, nearly 19% of each station, while pasture and hayland composed nearly 15% of the area of each station on average. Least

Table 7. Means and standard errors (SE) for percent of transect in corn, garden, wheat, soybeans, truck crops, tobacco, bare ground, grain/hay, miscellaneous crops, and unknown crop types. Annual values are based on 121 stations sampled along 10 transects 1986-1991, Halifax County, Virginia.

Crop	Year												p ^c	
	1986		1987		1988		1989		1990		1991			
	X	SE	X	SE	X	SE	X	SE	X	SE	X ^a	SE	MRPP ^b	
Corn	4.16a	0.85	2.33ab	0.78	1.88b	0.55	1.10bc	0.37	0.74c	0.51	1.22bc	0.42	-5.02	<0.001
Garden	0.63a	0.12	0.48a	0.18	0.59a	0.14	0.60a	0.11	0.51a	0.10	0.53a	0.10	0.55	0.67
Wheat	1.63a	0.53	1.60a	0.48	2.19a	0.66	0.73a	0.25	1.40a	0.57	2.38a	0.64	-0.14	0.38
Soybeans	1.43	0.49	1.29a	0.43	0.92a	0.38	1.18a	0.48	0.33a	0.19	0.68a	0.24	-0.04	0.42
Unknown	0.09a	0.03	0.04ac	0.02	0.0b	0.0	0.0bc	0.0	0.0b	0.0	0.0b	0.0	-4.6	<0.01
Truck crops	0.37a	0.36	0.32a	0.30	0.28a	0.21	0.27a	0.22	0.19a	0.16	0.24a	0.20	1.77	1.0
Tobacco	1.47a	0.31	2.02a	0.44	2.24a	0.45	2.46a	0.53	2.98a	0.57	2.64a	0.50	0.13	0.49
Bare ground	0.92ab	0.28	1.09bc	0.24	0.53ac	0.12	0.24a	0.16	1.92b	0.43	0.44ac	0.24	-5.0	<0.001
Grain/hay	0.0a	0.0	0.62b	0.19	0.03a	0.03	0.0a	0.0	0.0a	0.0	0.0a	0.0	-9.20	<0.001
Misc.	0.85a	0.41	0.22a	0.11	0.23a	0.14	0.15a	0.12	0.05a	0.03	0.41a	0.27	-0.49	0.26

^aMeans within a row not sharing a common letter are different ($P < 0.01$). Pairwise comparisons were performed using Multiple Response Permutations Procedures running on Blossom Statistical Software (1992). Sample sizes for all comparisons was 60.

^bStandardized test statistic for MRPP test.

^cProbability that ≥ 1 of the means differs from the rest.

represented were grazed woodlands. Fourteen cover types accounted for slightly more than 2% of each station on average. The total area accounted for at a given station averaged 88%. This value is <100% because several cover types (residential areas, roads, ponds, etc.) were excluded in the evaluation of the model; data for the model test for these cover types either were unavailable or not applicable. The distribution of these miscellaneous cover types was relatively constant across all 121 stations.

The majority of patches of each cover type averaged <3 ha in size. Mature woodlands with a lightly-stocked saw timber and medium-stocked sapling and pole components averaged 3.12 ha. Medium canopy woodlands averaged <1 ha in size. High canopy woodlands were nearly twice this size, on average (Table 2). There were 635 active cropfields distributed across the 121 stations. The mean size of these fields was just under 0.8 ha. Fallow fields and fallow fields with sapling regeneration averaged 0.8 and 0.86 ha in size, respectively. Pasture and hayfields were more than 2X the size of the average crop field (2.01 ha, Table 2).

I sampled a total of 220 vegetation plots distributed among the 28 cover types (Table 8). Except for the density of mast producing trees > 25.4 cm dbh, I generated estimates for all 8 model variables for all 28 cover types (Tables 9, 10, 11). The number of sites sampled per cover type varied from 8 (cutovers with

Table 8. Mean Life Requisite Suitability Index values for the northern bobwhite CRP HSI model for 28 cover types sampled 1986-1991, Halifax County, Virginia.

Habitat Type	n	Mean Life Requisite Suitability Index		
		Winter Food	Cover	Nest
Woodlands^a				
LOW CANOPY				
Saplings, light stocking	13	0.76 ^c	0.43	0.49
Cutover with Saplings, light stocking	8	0.85 ^c	0.84	0.25
Saplings, heavy stocking	14	0.67 ^c	0.51	0.25
Saplings, heavy stocking; Poles, light stocking	14	0.58 ^c	0.58	0.14
Cutover with Saplings, medium stocking; Poles light stocking	13	0.18	0.63	0.29
Low Canopy	62	0.61	0.60	0.28
MID CANOPY				
Saplings, light stocking; Poles medium stocking	15	0.05	0.54	-
Poles medium stocking	14	0.07	0.44	-
Saplings and Poles, medium stocking	14	0.06	0.44	-
Mid Canopy	43	0.06	0.47	-
HIGH CANOPY				
Saplings, Poles, and Mature, light stocking	10/25 ^d	0.37	0.36	- ^e
Poles and Mature, light stocking	12/33	0.26	0.33	-
Saplings and Pole medium stocking; Mature, light stocking	12/24	0.33	0.37	-

Table 8. Continued.

Habitat Type	n	Mean Life Requisite Suitability Index		
		Winter Food	Cover	Nest
High Canopy	44/103	0.30	0.36	-
Saplings, heavy stocking; Pole and Mature, light stocking	10/21	0.23	0.38	-
Saplings, Poles, and Mature, light stocking	15	0.31	0.14	-
Poles and Mature, light stocking	15	0.32 ^f	0.14	-
Saplings and Pole medium stocking; Mature, light stocking	15 ^g	0.30	0.14	-
Saplings, heavy stocking; Pole and Mature, light stocking	15	0.19	0.14	-
Saplings, light stocking	15	0.20	0.14	0.61
Cutover with Saplings, light stocking	15	0.20	0.14	0.61
Saplings, light stocking; Poles, medium stocking	15	0.20	0.14	-
Cutover with Saplings, medium stocking; Poles light stocking	15	0.20	0.14	0.61
Cutover with Saplings, medium stocking; Poles and Mature, light stocking	15	0.20	0.14	0.61
Saplings, heavy stocking	15	0.20	0.14	0.61
Poles, medium stocking	15	0.20	0.14	-
Saplings and Poles, medium stocking	15	0.20	0.14	-
Other Habitats				
Crop	20 ^h	0.82 ^c	ⁱ	0.33
Pasture/hayland	10	^j	-	0.47
Fallow crop field	13	0.70 ^c	-	0.42

Table 8. Continued.

Habitat Type	n	Mean Life Requisite Suitability Index		
		Winter Food	Cover	Nest
Fallow crop field with saplings, light stocking	15	0.67 ^c	0.14	0.57

^a See Figure 5 for the derivation of the Life Requisite Suitability Indices.

^b Woodlands were classified according to composition (saplings < 3cm dbh; 3 ≤ poles < 25 cm dbh; mature > 25 cm dbh) and relative stocking rates (light < 25%; 25 ≤ medium < 50; and heavy > 50 % coverage) in each size class. Stocking rates are an "ocular" estimate of % coverage.

^c Winter food SI equal to the SI for % canopy cover of late-winter foods (cclwfw, Table 11).

^d Sample sizes used to estimate all parameters excluding density of mast trees/samples used to estimate density of mast trees.

^e Cover type not considered a source of nest/brood habitat.

^f Densities in ungrazed equivalent of each woodland type were used in the estimate of the winter food LRSI.

^g A total of 15 sites was used to estimate conditions in all grazed woodlands

^h A total of 20 fields representing corn, wheat, soybeans, unknown, miscellaneous, truck, tobacco, and grain/hay was sampled.

ⁱ Cover type not considered a source of cover habitat.

^j Cover type not considered a source of winter food.

Table 9. Mean, standard error (SE), and mean Suitability Index (SIV5) for canopy cover of woody vegetation < 2 m in 28 cover types for 121 sites sampled 1986-1991, Halifax County, Virginia. This variable represents the cover life requisite of the Habitat Suitability Index (HSI) model for the northern bobwhite (Schroeder 1985).

Habitat Type	canopy cover of woody vegetation < 2 m		
	X	SE	SIV5
Woodlands^a			
LOW CANOPY			
Saplings, light stocking	18.8 ^b	4.8	0.43
Cutover with Saplings, light stocking	41.8	6.6	0.84
Saplings, heavy stocking	20.4	3.2	0.51
Saplings, heavy stocking; Poles, light stocking	13.5	3.3	0.33
Cutover with Saplings, medium stocking; Poles light stocking	27.1	4.9	0.63
Low Canopy	24.9	2.0	0.58
MID CANOPY			
Saplings, light stocking; Poles medium stocking	23.1	3.6	0.54
Poles medium stocking	17.6	3.0	0.44
Saplings and Poles, medium stocking	18.7	3.5	0.44
Mid Canopy	19.9	1.9	0.47
HIGH CANOPY			
Saplings, Poles, and Mature, light stocking	14.2	2.4	0.36
Poles and Mature, light stocking	13.5	3.3	0.33
Saplings and Pole medium stocking; Mature, light stocking	14.8	2.3	0.37
Saplings, heavy stocking; Pole and Mature, light stocking	15.2	2.0	0.38
High Canopy	14.4	1.3	0.34
Grazed Woodlands			
Saplings, Poles, and Mature, light stocking	5.5	1.7	0.14
Poles and Mature, light stocking	5.5 ^c	1.7	0.14
Saplings and Pole medium stocking; Mature, light stocking	5.5	1.7	0.14
Saplings, heavy stocking; Pole and Mature, light stocking	5.5	1.7	0.14
Saplings, light stocking	5.5	1.7	0.14
Cutover with Saplings, light stocking	5.5	1.7	0.14

Table 9. Continued.

Habitat Type	canopy cover of woody vegetation < 2 m		
	X	SE	SIV5
Saplings, light stocking; Poles, medium stocking	5.5	1.7	0.14
Cutover with Saplings, medium stocking; Poles light stocking	5.5	1.7	0.14
Cutover with Saplings, medium stocking; Poles and Mature, light stocking	5.5	1.7	0.14
Poles, medium stocking	5.5	1.7	0.14
Saplings and Poles, medium stocking	5.5	1.7	0.14
Other Habitats			
Crop	0.0	0.0	0.0
Pasture/hayland	0.6	0.3	0.02
Fallow crop field	4.9	2.3	0.12
Fallow crop field with saplings, light stocking	5.6	1.6	0.14

^aWoodlands were classified according to composition (saplings < 3cm dbh; 3 ≤ poles < 25 cm dbh; mature > 25 cm dbh) and relative stocking rates (light < 25%; 25 ≤ medium < 50; and heavy > 50 % coverage) in each size class. Stocking rates are an "ocular" estimate of % coverage.

^bSee table 2 for sample sizes used to estimate means.

^cA total of 15 "grazed" woodlands was sampled. Grazed woodlands were initially treated as a single cover type because of little if any differences in the understories. However, because of differences in mast availability, I subsequently reclassified each stand based on tree stocking rates and sizes.

Table 10. Means, standard errors (SE), and mean Suitability Indices (SIV1, 2, 3, and 4) for density of mast trees > 25.4 cm dbh/ha, % bare or lightly-littered ground (grmidf), % canopy cover of herbaceous quail foods, and % canopy cover of late winter quail foods in 28 cover types for 121 sites sampled 1986-1991, Halifax County, Virginia. These variables represent the winter food life requisite of the Habitat Suitability Index (HSI) model for the northern bobwhite (Schroeder 1985).

Habitat Type	density of mast trees > 25.4 cm dbh			% bare or lightly-littered ground			% canopy cover of herbaceous quail foods			% canopy cover of late-winter quail foods		
	X	SE	SIV4	X	SE	SIV3	X	SE	SIV2	X	SE	SIV1
Woodlands^a												
LOW CANOPY												
Saplings, light stocking	0.0 ^c	0.0	0.0	67.1	7.6	0.59	28.8	6.2	0.75	28.8	6.2	0.76
Cutover with Saplings, light stocking	0.0	0.0	0.0	67.8	13.3	0.37	26.8	4.6	0.85	26.8	4.6	0.85
Saplings, heavy stocking	0.0	0.0	0.0	66.1	7.5	0.58	27.7	6.8	0.67	27.7	6.8	0.67
Saplings, heavy stocking; Poles, light stocking	0.0	0.0	0.0	81.0	6.2	0.34	15.9	3.6	0.58	15.9	3.6	0.58
Cutover with Saplings, medium stocking; Poles light stocking	0.0	0.0	0.0	87.4	4.5	0.28	24.2	3.2	0.82	24.2	3.2	0.83
Low Canopy	0.0	0.0	0.0	74.4	3.4	0.44	24.4	2.4	0.72	24.4	2.4	0.72
MID CANOPY												
Saplings, light stocking; Poles medium stocking	0.0	0.0	0.0	93.7	2.3	0.16	8.5	1.5	0.41	8.5	1.5	0.41
Poles medium stocking	0.0	0.0	0.0	84.6	6.6	0.23	10.3	3.4	0.40	10.3	3.4	0.40
Saplings and Poles, medium stocking	0.0	0.0	0.0	92.1	5.2	0.13	8.3	1.8	0.4	8.3	1.8	0.40
Mid Canopy	0.0	0.0	0.0	90.2	2.9	0.17	9.0	1.3	0.40	9.0	1.3	0.40
HIGH CANOPY												
Saplings, Poles, and Mature, light stocking	101.3 ^d	13.3	0.53	52.8	2.0	0.98	12.0	4.5	0.45	12.0	4.5	0.45
Poles and Mature, light stocking	110.4	15.1	0.57	79.5 ^e	6.0	0.47	10.2	3.5	0.42	10.2	3.5	0.42

Table 10. Continued.

Habitat Type	density of mast trees > 23.4 cm dbh			% bare or lightly-littered ground			% canopy cover of herbaceous quail foods			% canopy cover of late-winter quail foods		
	\bar{X}	SE	SIV4	\bar{X}	SE	SIV3	\bar{X}	SE	SIV2	\bar{X}	SE	SIV1
Saplings and Pole medium stocking; Mature, light stocking	103.5	18.4	0.50	51.8	1.2	1.01	8.6	3.3	0.37	8.6	3.3	0.37
Saplings, heavy stocking; Pole and Mature, light stocking	28.2	7.4	0.17	64.2	6.4	0.76	11.4	3.2	0.48	11.4	3.2	0.48
High Canopy	84.6	7.4	0.43	62.9	2.9	0.78	10.5	1.8	0.43	10.5	1.8	0.43
Grazed Woodlands												
Saplings, Poles, and Mature, light stocking	101.31	13.3	0.53	39.9	6.8	0.71	10.0	3.1	0.42	10.0	3.1	0.42
Poles and Mature, light stocking	110.4	15.1	0.57	39.9	6.8	0.71	10.0	3.1	0.42	10.0	3.1	0.42
Saplings and Pole medium stocking; Mature, light	103.5	18.4	0.50	39.9	6.8	0.71	10.0	3.1	0.42	10.0	3.1	0.42
Saplings, heavy stocking; Pole and Mature, light	28.2	7.4	0.17	39.9	6.8	0.71	10.0	3.1	0.42	10.0	3.1	0.42
Saplings, light stocking	0.0	0.0	0.0	39.9	6.8	0.71	10.0	3.1	0.42	10.0	3.1	0.42
Cutover with Saplings, light stocking	0.0	0.0	0.0	39.9	6.8	0.71	10.0	3.1	0.42	10.0	3.1	0.42
Saplings, light stocking; Poles, medium stocking	0.0	0.0	0.0	39.9	6.8	0.71	10.0	3.1	0.42	10.0	3.1	0.42
Cutover with Saplings, medium stocking; Poles light	0.0	0.0	0.0	39.9	6.8	0.71	10.0	3.1	0.42	10.0	3.1	0.42
Cutover with Saplings, medium stocking; Poles and Mature, light stocking	0.0	0.0	0.0	39.9	6.8	0.71	10.0	3.1	0.42	10.0	3.1	0.42
Saplings, heavy stocking	0.0	0.0	0.0	39.9	6.8	0.71	10.0	3.1	0.42	10.0	3.1	0.42
Poles, medium stocking	0.0	0.0	0.0	39.9	6.8	0.71	10.0	3.1	0.42	10.0	3.1	0.42
Saplings and Poles, medium stocking	0.0	0.0	0.0	39.9	6.8	0.71	10.0	3.1	0.42	10.0	3.1	0.42

Table 10. Continued.

Habitat Type	density of mast trees > 25.4 cm dbh			% bare or lightly- littered ground			% canopy cover of herbaceous quail foods			% canopy cover of late-winter quail foods		
	\bar{X}	SE	SIV4	\bar{X}	SE	SIV3	\bar{X}	SE	SIV2	\bar{X}	SE	SIV1
Other Habitats												
Crop	0.0	0.0	0.0	81.5	4.9	0.37	50.7	7.7	0.74	50.7	7.7	0.82
Pasture/hayland	0.0	0.0	0.0	38.4	7.7	0.75	6.8	3.0	0.32	6.8	3.0	0.32
Fallow crop field	0.0	0.0	0.0	34.8	8.2	0.64	28.3	6.5	0.70	28.3	6.5	0.70
Fallow crop field with saplings, light stocking	0.0	0.0	0.0	45.5	6.4	0.78	30.7	7.1	0.67	30.7	7.1	0.67

*Woodlands were classified according to composition (saplings < 3cm dbh; 3 ≤ poles < 25 cm dbh; mature > 25 cm dbh) and relative stocking rates (light < 25%; 25 ≤ medium < 50; and heavy > 50 % coverage) in each size class. Stocking rates are an "ocular" estimate of % coverage.

^bSee Table 3 for sample sizes used to estimate means.

^cMean densities for the 4 mast-producing, grazed woodland habitats are equal to the non-grazed equivalent, rather than the mean based on the estimates from the 15 grazed woodlands, since the latter includes several non-mast producing habitats.

^dA total of 15 grazed woodlands was sampled. Grazed woodlands were initially treated as a single cover type because of little if any differences in the understories. However, because of differences in mast availability, I subsequently reclassified each stand based on tree stocking rates and sizes.

Table 11. Means, standard errors (SE), and mean suitability indices (SI) for percent herbaceous canopy cover, percent bare or lightly-littered ground, and percent of the herbaceous canopy composed of grass in 28 cover types for 121 sites sampled 1986-1991, Halifax County, Virginia. These variables represent the nest/brood life requisite of the CRP HSI model for the northern bobwhite.

Habitat Type	% herbaceous canopy cover			% bare or lightly-littered ground			% of herbaceous canopy that is grass		
	\bar{X}	SE	SIV7	\bar{X}	SE	SIV8	\bar{X}	SE	SIV6
Woodlands^a									
LOW CANOPY WOODLANDS									
Saplings, light stocking	50.3 ^b	8.3	0.66	67.1	7.6	0.63	45.7	9.8	0.63
Cutover with Saplings, light stocking	25.0	10.6	0.29	67.8	13.3	0.42	53.0	13.4	0.66
Saplings, heavy stocking	29.4	9.4	0.28	66.1	7.5	0.60	53.3	10.7	0.58
Saplings, heavy stocking; Poles, light stocking	17.7	6.7	0.18	81.0	6.2	0.43	42.1	10.6	0.54
Cutover with Saplings, medium stocking; Poles light stocking	24.2	6.3	0.34	87.4	4.5	0.38	73.2	6.4	0.79
Low Canopy Woodlands	29.5	3.8	0.35	74.4	3.4	0.50	53.3	4.6	0.64
MID CANOPY WOODLANDS									
Saplings and Poles, medium stocking	11.9	6.3	0.06	92.1	5.18	0.36	45.4	10.9	1.0
Saplings, light stocking; Poles medium stocking	10.8	3.0	0.13	93.7	2.3	0.23	44.1	10.5	0.54
Poles medium stocking	34.9	8.8	0.43	84.6	6.6	0.30	56.6	10.1	0.65
Mid Canopy Woodlands	18.9	0.20	0.20	90.2	2.85	0.24	48.6	6.0	0.59
HIGH CANOPY WOODLANDS									
Saplings, Poles, and Mature, light stocking	17.4	9.4	0.17	52.8	2.0	0.98	38.8	15.1	0.35
Poles and Mature, light stocking	28.5	9.4	0.31	79.5	6.0	0.50	48.0	11.0	0.61

Table 11. Continued.

Habitat Type	% herbaceous canopy cover			% bare or lightly-littered ground			% of herbaceous canopy that is grass		
	\bar{X}	SE	SIV7	\bar{X}	SE	SIV8	\bar{X}	SE	SIV6
Saplings and Pole medium stocking; Mature, light stocking	21.6	9.3	0.29	51.8	1.2	1.0	35.3	13.7	0.41
Saplings, heavy stocking; Pole and Mature, light stocking	20.0	3.2	0.32	64.2	6.4	0.78	51.6	7.8	0.82
High Canopy Woodlands	22.2	4.1	0.27	62.9	2.9	0.80	43.6	5.9	0.55
Grazed Woodlands									
Saplings, Poles, and Mature, light stocking	66.4	6.0	0.74	39.9	6.8	0.71	69.3	6.2	0.82
Poles and Mature, light stocking	66.4 ^c	6.0	0.74	39.9	6.8	0.71	69.3	6.2	0.82
Saplings and Pole medium stocking; Mature, light stocking	66.4	6.0	0.74	39.9	6.8	0.71	69.3	6.2	0.82
Saplings, heavy stocking; Pole and Mature, light stocking	66.4	6.0	0.74	39.9	6.8	0.71	69.3	6.2	0.82
Saplings, light stocking	66.4	6.0	0.74	39.9	6.8	0.71	69.3	6.2	0.82
Cutover with Saplings, light stocking	66.4	6.0	0.74	39.9	6.8	0.71	69.3	6.2	0.82
Saplings, light stocking; Poles, medium stocking	66.4	6.0	0.74	39.9	6.8	0.71	69.3	6.2	0.82
Cutover with Saplings, medium stocking; Poles light	66.4	6.0	0.74	39.9	6.8	0.71	69.3	6.2	0.82
Cutover with Saplings, medium stocking; Poles and Mature, light stocking	66.4	6.0	0.74	39.9	6.8	0.71	69.3	6.2	0.82
Saplings, heavy stocking	66.4	6.0	0.74	39.9	6.8	0.71	69.3	6.2	0.82
Poles, medium stocking	66.4	6.0	0.74	39.9	6.8	0.71	69.3	6.2	0.82

Table 11. Continued.

Habitat Type	% herbaceous canopy cover			% bare or lightly-littered ground			% of herbaceous canopy that is grass		
	\bar{X}	SE	SIV7	\bar{X}	SE	SIV8	\bar{X}	SE	SIV6
Saplings and Poles, medium stocking	66.4	6.0	0.74	39.9	6.8	0.71	69.3	6.2	0.82
Other Habitats									
Crop	63.9	7.4	0.57	81.5	4.91	0.44	81.1	6.7	0.64
Pasture/hayland	92.0	4.4	0.51	38.4	7.7	0.69	87.4	3.4	0.73
Fallow crop field	78.8	7.1	0.57	34.8	8.2	0.6	47.8	9.7	0.65
Fallow crop field with saplings, light stocking	69.7	7.0	0.65	45.5	6.4	0.78	50.3	8.4	0.72

^aWoodlands were classified according to composition (saplings < 3cm dbh; 3 ≤ poles < 25 cm dbh; mature > 25 cm dbh) and relative stocking rates (light < 25%; 25 ≤ medium < 50; and heavy > 50 % coverage) in each size class. Stocking rates are an "ocular" estimate of % coverage.

^bSee table 2 for sample sizes used to estimate means.

^cA total of 15 "grazed" woodlands was sampled. Grazed woodlands were initially treated as a single cover type because of little if any differences in the understories. However, because of differences in mast availability, I subsequently reclassified each stand based on tree stocking rates and sizes.

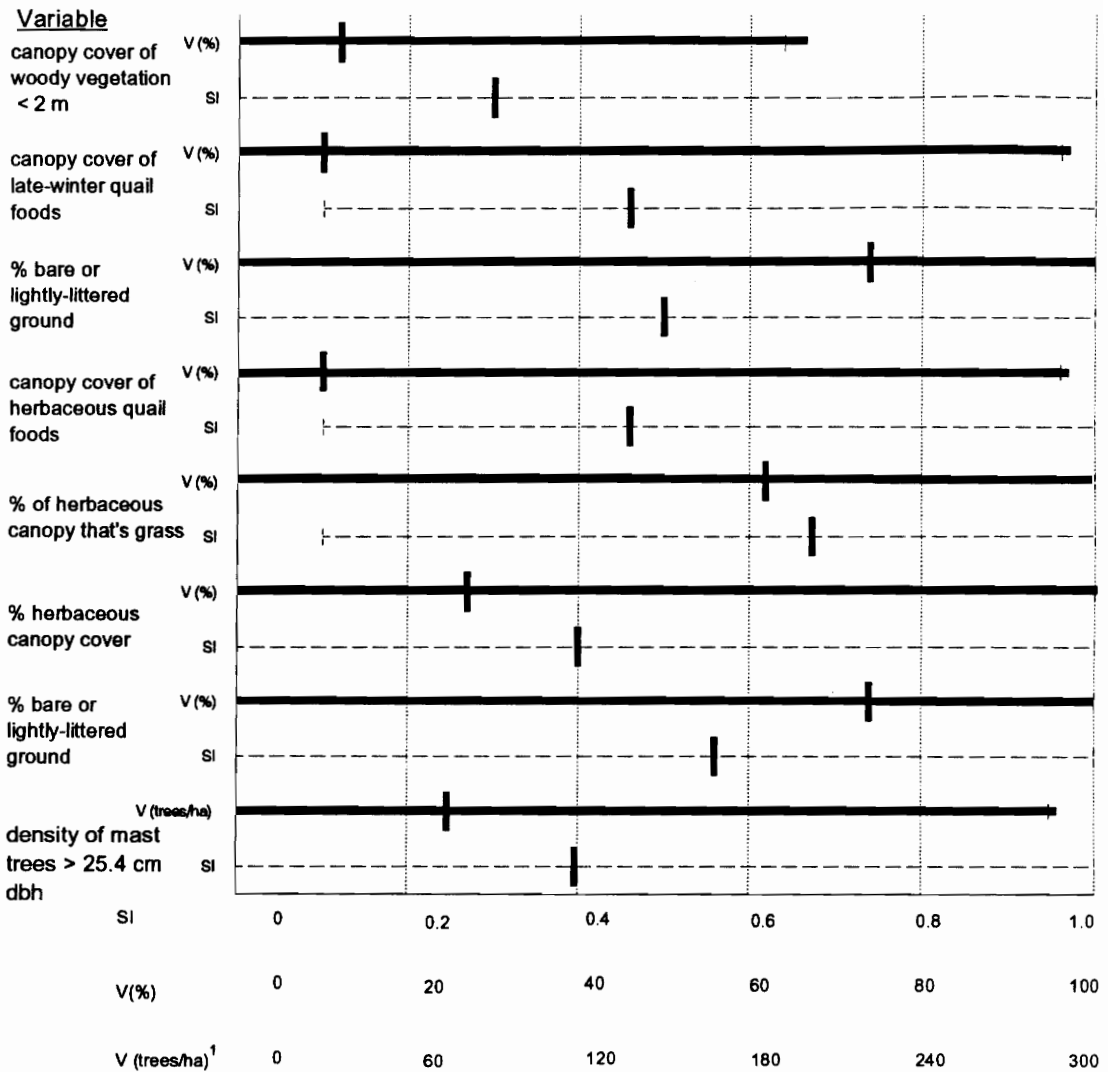
sapling regeneration) to 15 for several woodland and grazed woodland habitats. For all variables except cc5_2, the range of conditions represented in the sample was \geq 90% of the possible values (0 - 100%). The density of woody vegetation $<$ 2 m ranged from 0 to just over 60% (Fig. 7). The 3 variables representing the nest/brood habitat component covered the entire range of values possible. As is evident by the location of the median values (Fig. 7), most of the distributions were skewed. Median values for canopy cover of woody vegetation $<$ 0.5-2 m, canopy cover of late-winter foods, canopy cover of herbaceous quail foods, and canopy cover of herbaceous vegetation were $<$ 50%. Medians for percent bare or lightly-littered ground were just over 70%, while the median for percent of herbaceous canopy that is grass was just over 60%.

The number of sites sampled for purposes of estimating the density of mast for trees $>$ 25.4 cm dbh varied from 21 to 33 (Table 8). The density of mast trees $>$ 25.4 cm dbh was estimated in only 4 cover types, for a total of 103 sites sampled. This variable ranged from 0 to just under 300 trees/ha. (Table 2).

HSI Value Determination

Individual Variable Suitability Indices

Observed individual variable SI values spanned the entire range of possible



¹ trees > 25.4 cm dbh

Figure 7. Range (horizontal line) and median values (vertical line) for 8 variables (solid lines) representing the cover (canopy cover of woody vegetation <2 m , winter food (canopy cover of late-winter quail foods, % bare or lightly-littered ground, canopy cover of herbaceous quail foods, density of mast trees >25.4 cm dbh) and nest/brood (% of herbaceous canopy that is grass, % herbaceous canopy cover, and % bare or lightly-littered ground) life requisites composing the northern bobwhite CRP model. Values for all variables but density of mast trees >25.4 cm dbh are based on 220 plots representing 28 cover types. Estimates for the latter are based on 120 plots in four cover types. Data were collected summer 1991, Halifax County, Virginia. Values for the mean SI for each variable are also shown. 67

values for all 8 variables sampled (Fig. 7). Although some of the SIs had skewed distributions, most notable of which was cc5_2, distributions of the SIs were more even than the variables from which they were derived (Fig. 7). Median values for the 8 SIs ranged from 0.3 for cc5_2 to 0.7 for vrcgr01 (Fig. 7).

There was considerable variation in the quality of winter food, nest/brood habitat, and cover provided by the 28 cover types sampled (Table 8). The mean LRSI for winter food ranged from 0.05 to 0.85. Mid canopy woodlands with light and medium stocking in the sapling and pole components, respectively, provided the least amount of winter food. Cutovers with light sapling regeneration provided the greatest amount of winter food (Table 8). Crop fields represented a source of high quality winter foods as well. The mean LRSI for winter food in crop fields was 0.82. Of the 3 general woodland classes, early successional woodlands provided the greatest amount of winter food. The mean LRSIs for these 3 general classes were 0.61, 0.06, and 0.30, low, mid, and high canopy, respectively. Although, mid-canopy woodlands were consistently poor in terms of the winter food component, early successional woodlands were consistently relatively high. A notable exception was older clearcuts with heavy sapling regeneration and lightly stocked pole timber. Grazed woodlands were generally relatively poor providers of winter food for the bobwhite; values for the winter food LRSI ranged from 0.19 to 0.32. Fallow

agricultural fields with and without sapling regeneration provided slightly less winter food than cropfields but were of similar quality as early successional woodland habitats. Pasture and hayland contributed nothing to the estimate of available winter food. In general, the early successional habitats were of the highest quality in terms of estimated available winter food. These cover types, most notably the low canopy woodlands, represented some of the potentially best overall quail habitat on the study area. Although none of the 5 habitat types in the low canopy woodland group provided optimum conditions for any of the life requisites, they did provide winter food, cover, and nest/brood habitat at levels > 0 . Their grazed counterparts were the only other cover types that provided all 3 life requisites. However, while the grazed low canopy woodlands provided apparently better quality nest habitat than their ungrazed equivalents, winter food and cover were of much higher quality in the ungrazed woodlands. Moreover, the mean LRSI for nest/brood habitat, while less than the 0.61 reported for the grazed woodlands, ranged from 0.14 to 0.49.

Relative to winter food, mean LRSI values for cover were somewhat more uniform, at least among the woodland habitats. Low canopy woodlands provided the greatest amount of cover on average (0.60), than either mid or high canopy woodlands. Mean LRSIs for cover for these 3 groups of habitats were 0.6, 0.47, and 0.36, low, mid, and high canopy woodlands, respectively. Regeneration cuts with

saplings, the greatest source of winter food, also provided the greatest amount of cover (Table 8). The mean LRSI for this cover type was 0.84. Crops, fallow crop fields, and pastures provided no cover for the bobwhite while grazed woodlands were of relatively poor quality (Table 8) with a mean LRSI of 0.14.

One half of the cover types on the study area were not considered potential sources of nest/brood habitat (Table 8). Grazed and ungrazed mid and high canopy woodlands were assumed to provide no nest/brood habitat. Grazed early successional woodlands were the single best potential source of nest/brood habitat. The mean LRSI for these cover types was 0.61. Fallow agricultural fields with sapling regeneration were of comparable quality at 0.57 (Table 8). The remaining habitat types including crop fields, idle fields, pasture/hayland, and early successional woodlands were all of relatively low potential. The LRSI values for these cover types ranged from 0.14 for low canopy woodlands with a dense sapling component and a lightly-stocked pole component, to 0.47 for pastures and haylands. The marginal quality of pastures and hayfields was due largely to the amount of herbaceous vegetation. The SI for percent canopy cover of herbaceous vegetation was 0.51 (Table 10). The limiting factor in low canopy grazed woodlands was bare ground (SI = 0.71). However, in fallow fields with sapling regeneration, an excess of herbaceous vegetation reduced the potential of this habitat for nesting and

brooding bobwhites (Table 10).

Equivalent Percent and Composition Suitability Indices

Equivalent percent values for winter food, cover, and nest/brood habitat had similar distributions (Fig. 8). Values for each of these variables ranged from 1.44% (nest/brood habitat) to 62.4% (winter food). The composition SI indices for each of these variables ranged from 0.06 for winter food to 1 for both cover and nest/brood habitat. The maximum value for winter food was 0.78. The distributions for both cover and nest/brood Composition SIs were highly skewed. Each SI had a median of 1 (Fig. 8). Winter food was identified as the limiting life requisite at 115 of the 121 stations (Appendix Table 1). Nest/brood habitat and cover were the limiting life requisite at 3 stations each.

Model Performance

The number of quail detected at a station and model output were not correlated ($r_s = 0.09$, $P = 0.31$, Fig. 9). If we assume, at least temporarily, that the performance measure was in fact a reflection of potential population performance at each station, then the model failed. There are 3 general reasons why this may have occurred. First, models fail because they are inadequate representations of the

Equivalent Percent

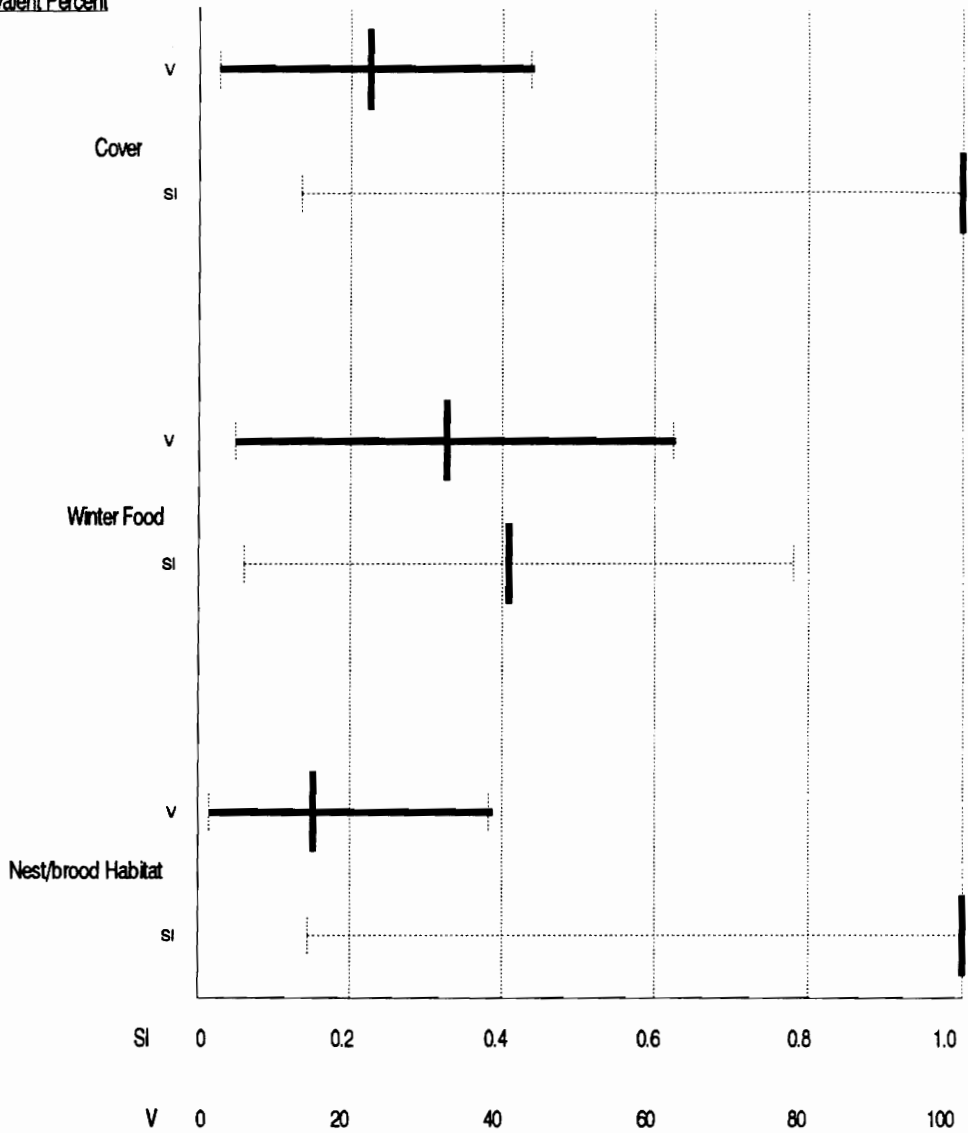


Figure 8. Range (horizontal line) and median (vertical bar) for equivalent percent of station providing optimum cover (solid line), winter food, and nest/brood habitat and their associated Suitability Indices (dotted line). Estimates are based on conditions at 121 sites sampled 1986-1991, Halifax County, Virginia.

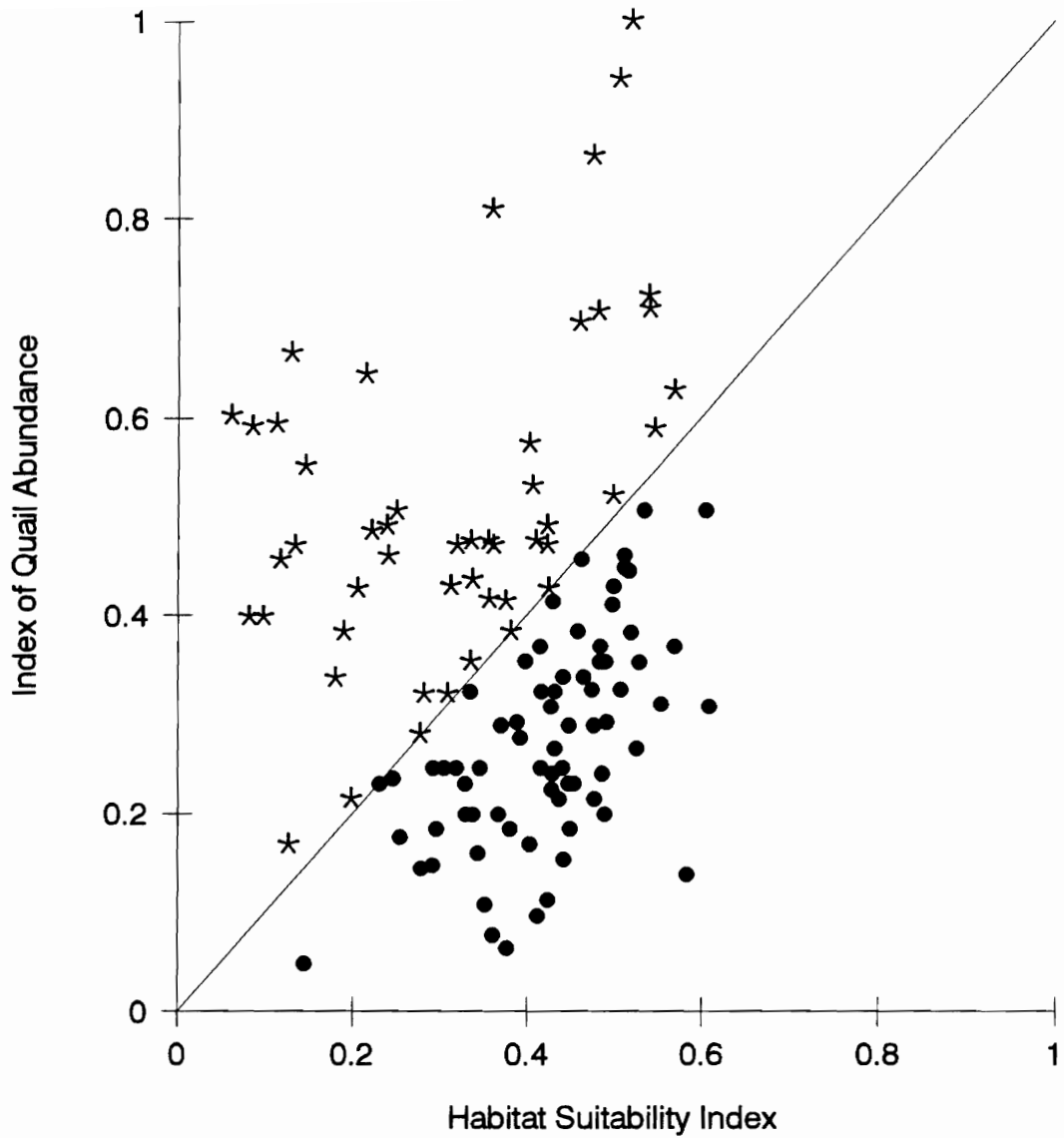


Figure 9. Relationship ($r_s = 0.09$, $P = 0.31$) between the performance measure and model output for 121 sites sampled 1986-1991, Halifax County, Virginia. The 45° line represents a habitat-imposed upper limit to population performance. Asterisks indicate those sites where population performance exceeded levels indicated by the model.

system being modeled. Second, poor study design may lead to negative or neutral results. This might include excessive sampling error due to limited data, the failure to acknowledge critical mathematical and statistical assumptions, improper analyses, poorly defined objectives, and in general, an improper application of the model. Third, failure may be due to an inadequate test (Terrell 1984). In those cases, deviations from predicted values are assumed to be due to variables external to the model that are influencing the performance measure. However, only through strong inference, i.e., by identifying the contributions of poor study design and model inadequacies to model performance, will it be possible to estimate the extent to which factors external to the model may have influenced the results. The remainder of this analysis attempts to determine what role faulty design and model inadequacies might have played in the present model test. A series of explanations (hypotheses) are proposed and each is examined for its potential contribution to the observed lack of fit of the model to the present data set.

Each of the 8 SI curves composing the CRP HSI model represent hypothesized habitat-imposed upper limits to population performance. Because habitat is not the only factor that has the potential to limit population performance, performance below levels indicated by each curve is anticipated and acceptable. However, when population performance exceeds levels indicated by the model, these

hypotheses are falsified. Consequently, while the rank correlation between model output and the performance measure (r_s) will be used as a criterion for adopting proposed changes, the principal standard by which proposed model changes will be evaluated will be their ability to account for the inconsistencies between actual population performance and levels indicated by the model.

Winter food determined model scores at all but 6 of the 121 stations. Thus, the absence of a relationship ($r_s = 0.09$, $P = 0.33$, $n = 121$) between model output and the performance measure translates to no relationship between available winter food and the performance measure (Fig. 10). Consequently, an improved model fit will be realized only if it is possible to improve the relationship between estimates of available winter food and the number of whistling males detected at each station. The alternative is to demonstrate that the absence of a relationship is due to the fact that winter food was not limiting population performance. This possibility will be addressed later as well.

IMPROVING MODEL FIT: POTENTIAL SOURCES OF ERROR

Winter Food Component

If the fit of the model is to be improved, changes to the winter food component undoubtedly will be necessary. Not only was there no relationship

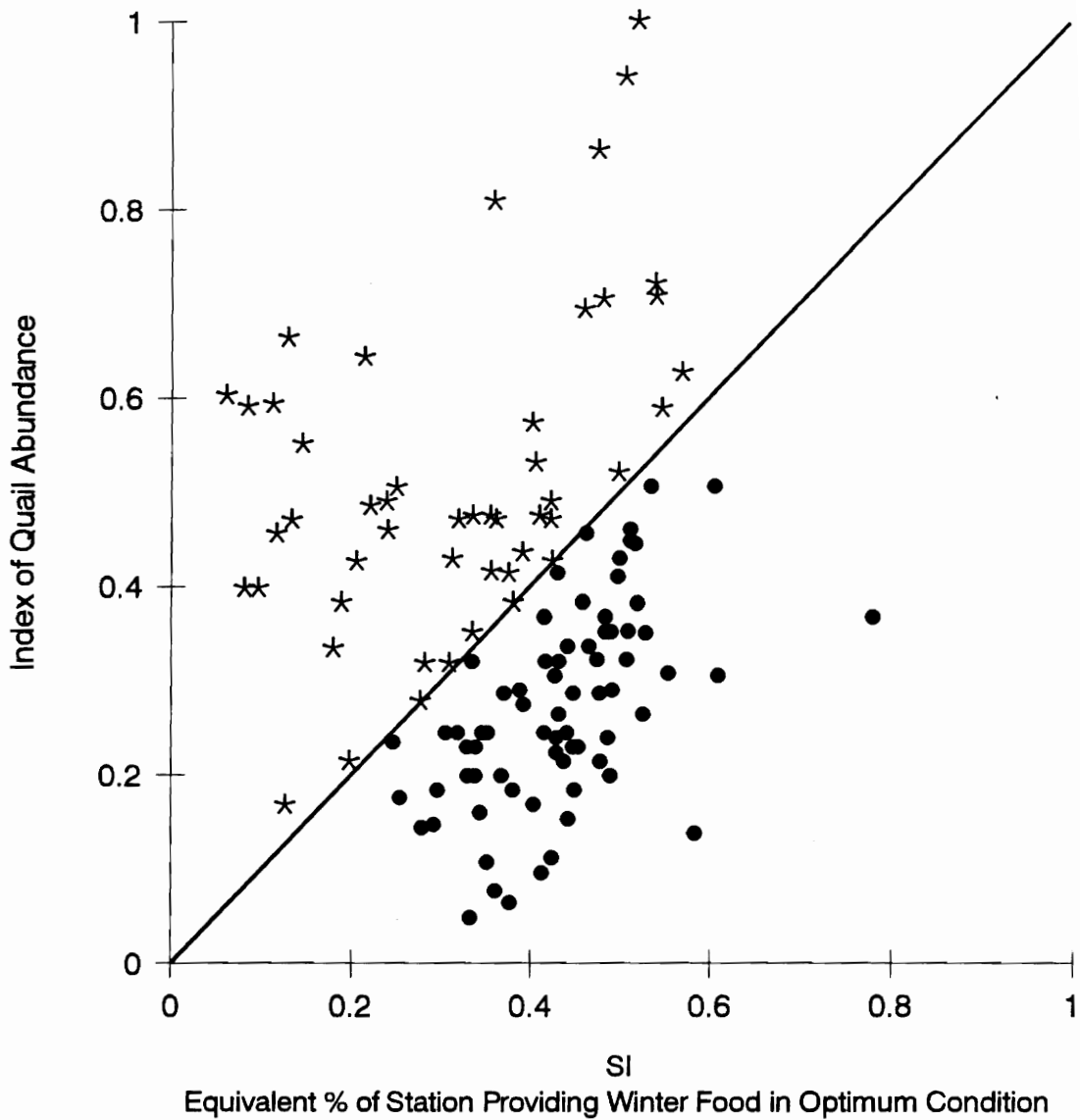


Figure 10. Relationship ($r_s = 0.09$, $P = 0.35$) between the performance measure and the Composition Suitability Index for equivalent percent of station providing winter food in optimum condition for 121 sites sampled 1986-1991, Halifax County, Virginia. The 45° line represents a habitat-imposed upper limit to population performance. Asterisks indicate sites where population performance exceeded levels indicated by the CRP HSI model.

between the SI for equivalent optimum winter food and the performance measure ($r_s = 0.09$, $P = 0.35$), population performance exceeded levels indicated by the model at 49 stations (Fig. 10). Thus, if an improved fit is to be realized, it will be necessary to modify the winter food component in such a way that model scores for those stations above the 45° line in Figure 10 reflect the level of quality existing at those sites.

Furthermore, although the points below the curve are of less concern, it may be that their distribution is not entirely a result of limiting factors external to the model. Specifically, the possibility does exist that the model may be overestimating the actual quality of the habitat under certain conditions. Thus, I hypothesize that the distribution of points below the curve in Figure 10 is partially due to the fact that one or more of the habitat types initially assumed to be providing winter food, was not. The converse is postulated for the points above the line in Figure 10. Specifically, I hypothesized that their position is a result of the failure of the model to identify ≥ 1 habitats providing winter food. Presumably, habitats responsible for the underestimate of winter food would be relatively rare at stations where performance fell short of levels indicated by the model. Similarly, it is expected that if there are habitats contributing to the overestimate of habitat quality, they would be relatively rare at stations represented by those points above the 45° line in Figure 10.

Logically then, the difference between the level of performance indicated by the model and that actually observed, hereafter referred to as the residual, should be correlated with area estimates for those habitats believed to be contributing to the residual. This holds for the group of stations above and below the 45° line. Otherwise, changes to the winter food component would be of little or no value (Fig. 11).

In summary, I propose that for those sites where there were more quail observed than indicated by the model, that an unaccounted food source may be present. If such a source exists, its addition to the estimate of winter food (OPTLWF) would shift the point to the right of its present location and subsequently move that site to a level more consistent with observed population values.

Alternative Sources of Winter Food

As proposed, the most likely explanation for the residual at those stations where population performance exceeded levels indicated by the model, was the failure to include ≥ 1 habitat types in the estimate of equivalent percent of the station providing winter food in optimum condition (OPTLWF) that were in fact sources of

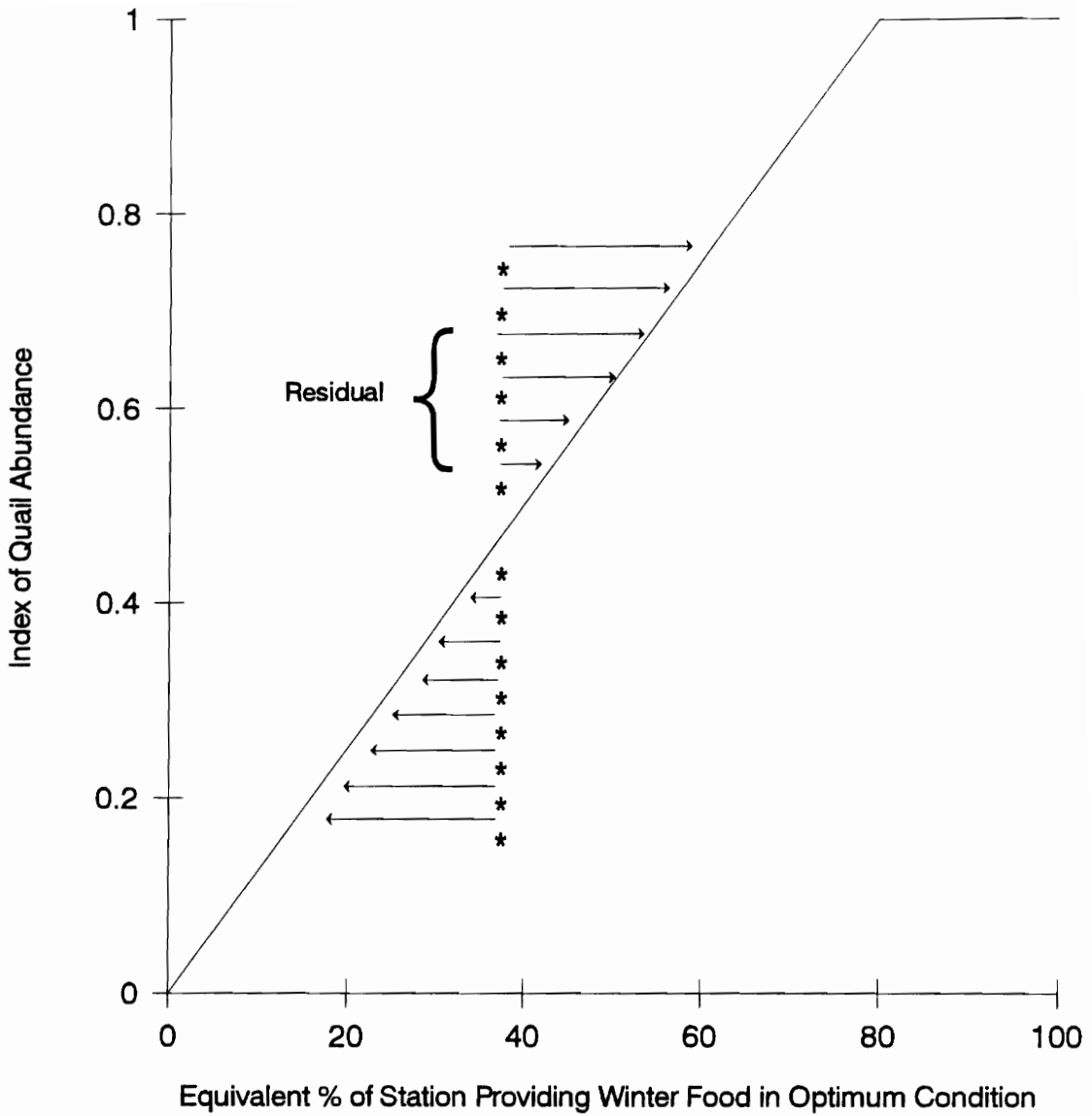


Figure 11. It is hypothesized that the difference between observed and predicted levels of performance (residual) for stations where performance exceeded levels indicated by the model, is due to the exclusion of one or more habitats providing winter food. Including these habitats would improve model fit by moving these points to the right. Conversely, if habitats are eliminated from the estimate of available winter food that were incorrectly assumed to be source of such resources, points below the line should move as indicated.

winter food. Of the 28 cover types identified on the study area, pasture/hayland was the only habitat type not considered as a potential food source (Table 8). Schroeder (1985) did not consider this habitat type as a source of winter food. My data indicated otherwise. The mean winter food LRSI for pasture/hayland was 0.19. Thus, this habitat type may be contributing to observed population performance and its exclusion from OPLTWF may be contributing to the disparity between observed levels of population performance and those indicated by the model. Specifically, I hypothesized that at least some of the observed variation in population performance for a given level of winter food (Fig. 12), can be accounted for by the area of the station in pasture/hayland cover. I hypothesized that those sites above the 45° line had more pasture/hayland, on average, than those below the line.

The 49 stations with a higher quail index than indicated by the model had more pasture/hayland ($\bar{X} = 12.7$ vs 3.3 ha, $F = 38.32$, 1,114 df, $P < 0.001$, 2-group ANOVA for unequal sample sizes) than those stations where population levels were consistent with levels indicated by the model. Further, and more importantly, the percent of the station in pasture/hayland and the residual were correlated negatively ($r = -0.52$, $P = 0.001$). Since the residuals are negative (predicted-observed) for this group, a negative correlation implies that increases in pasture/hayland actually lead to an increase in the residual. Thus, pasture/hayland

was included in the revised estimate of OPTLWF.

Because the area of pasture/hayland for these stations where population performance was below levels indicated by model was > 0 ($\bar{X} = 3.3$ ha), including this habitat type in the estimate of OPTLWF will increase the difference between the observed number of quail and the level indicated by the model, because it increased model scores. However, if the change had a marked effect on stations where population levels exceeded levels indicated by the model, the action would be justified.

The addition of pasture to OPTLWF reduced the residuals for the group of stations where population performance exceeded levels indicated by the model from -0.20 to -0.14. However, the addition of pasture/hayland had the opposite effect on the group of stations with fewer quail than expected. The mean residual for this group increased from 0.16 to 0.18, as expected. This increase is the result of 1 of 2 factors: 1) pasture does not provide winter food or 2) pasture/hayland is likely a source of winter food and the difference between observed levels of performance and those indicated by the model may be due to any of several limiting factors not addressed by the model. The addition of pasture/hayland reduced the residuals for the group of stations where performance exceeded levels indicated by the model and improved the correlation (r_s) between OPTLWF and the performance measure

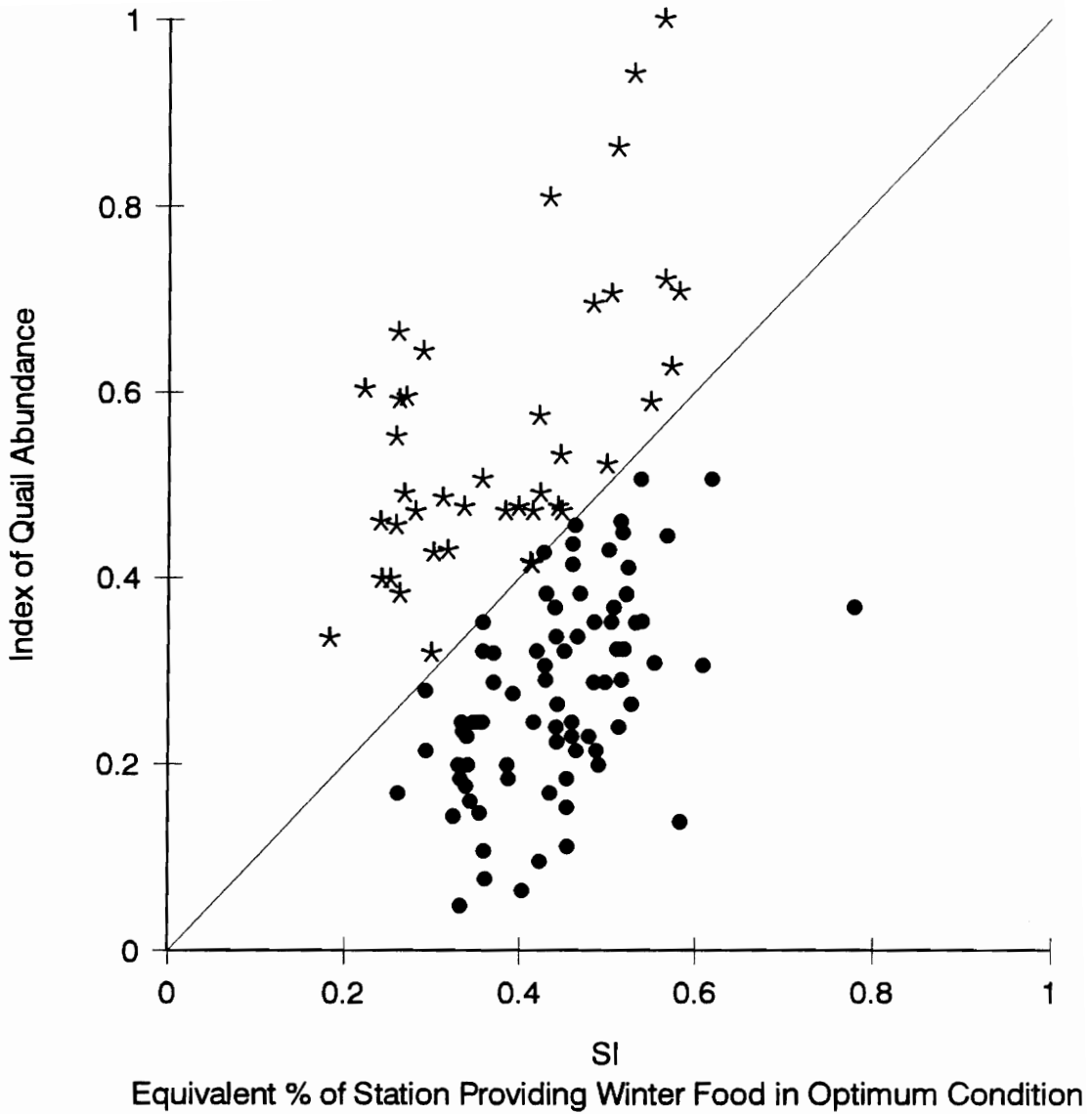


Figure 12. Relationship ($r_s = 0.13$, $P = 0.15$) between the performance measure and equivalent percent of station providing winter food in optimum condition for 121 sites sampled 1986-1991, Halifax County, Virginia. Pasture/hayland, not previously considered a source of winter food, contributed to the estimate of OPTLWF. Asterisks indicate sites where population performance exceeded levels indicated by the CRP HSI model.

from 0.09 ($P = 0.35$) to 0.13 ($P = 0.15$, Fig. 12). Furthermore, the area of a station in pasture/hayland was correlated positively with the performance measure ($r_s = 0.28$, $n = 121$, $P = 0.005$). Consequently, I believe the addition of pasture/hayland to the estimate of OPTLWF is a logical decision.

Habitat Interspersion

The HSI model for the northern bobwhite (Schroeder 1985) is 1 of several multi-cover type models developed by the U. S. Fish and Wildlife Service. For cover types unable to provide all 3 life requisites (nest/brood habitat, winter food, and cover), Schroeder assumed that the value of the resources present in the respective cover type(s) may be diminished if the cover type(s) is widely separated from the nearest source of the missing life requisite(s). Thus, the model by Schroeder uses an interspersion SI curve that relates distance between cover types and site quality. Sites lacking a life requisite but within 80 m of a cover type providing the missing life requisite are treated as if the missing life requisite were present (Fig. 13). Beyond this distance the estimated quality of the life requisites provided by the cover type lacking ≥ 1 life requisites is reduced according to Figure 13. Beyond 400 m the suitability of the site becomes zero.

The CRP model does not consider habitat interspersion. Consequently,

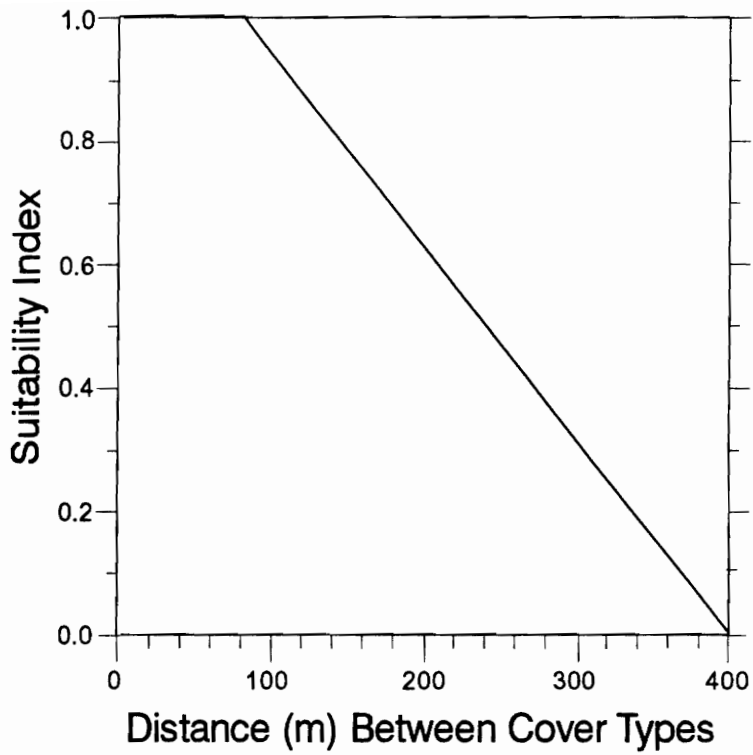


Figure 13. Relationship between habitat suitability and distance separating cover types lacking a given life requisite and those providing it. The curve is reproduced from the original HSI model by Schroeder (1985).

interspersion was not considered in the present test of the model. However, interspersion may be relevant, and as such, be partly responsible for the observed results. Because the inclusion of interspersion could only reduce model scores, i.e., move the position of all the points in Figure 10 to the left, the ideal situation would be to find that interspersion only was relevant at those stations where performance fell short of levels indicated by the model, with the converse being true for those stations where population performance exceeded levels indicated by the model. It is also expected that the residual (difference between observed population performance and levels indicated by the model) and an empirically-derived measure of interspersion be correlated positively.

To determine the distance between 2 cover types, Schroeder (1985) recommends randomly selecting 10 points within the cover type missing the life requisite(s), estimating the distance from each point to the nearest cover type providing the missing life requisite, and then use the mean distance in the suitability index curve for interspersion (Fig. 13). This suitability index then is multiplied by the relative area of the polygon lacking the life requisite, yielding "useable" area, which is then treated as if it were the relative area. I used PC ARC INFO to identify those cover types not providing all 3 life requisites and to estimate the distance to the nearest cover type providing the missing life requisite(s). These data were used

to generate an interspersion index which was an estimate of the percent of the station that would contribute less to estimates of ≥ 1 of the life requisites. In other words, if a habitat patch did not provide nest/brood habitat and the nearest source of this life requisite was 200 m away, the estimates for OPTLWF and OPTCOV for that patch would be reduced according to Figure 13. Estimates for both OPTLWF and OPTCOV would be approximately 60% of their original values.

Adjusting model scores to reflect the interspersion of cover types had little effect on model fit (Fig. 14). The correlation (r_s) between model output and the performance measure went from 0.12 based on the 115 stations for which interspersion data were available, $P = 0.21$) to 0.10 ($P = 0.29$, Fig. 14). Because winter food was the limiting factor at 97% of the stations, the lack of any relationship between model output and the performance measure was due to the fact that the availability of winter food appears to have had little to do with the observed distribution of quail ($r_s = 0.08$, $P = 0.41$, $n = 115$, Fig. 15).

That there was little improvement in the correlation between model output and the performance measure suggests that either 1) interspersion was not an issue (i.e., that there was little difference in model scores after adjusting for interspersion), 2) the suitability index curve for interspersion is incorrect, or 3) interspersion is irrelevant because nest/brood habitat or cover may have been driving

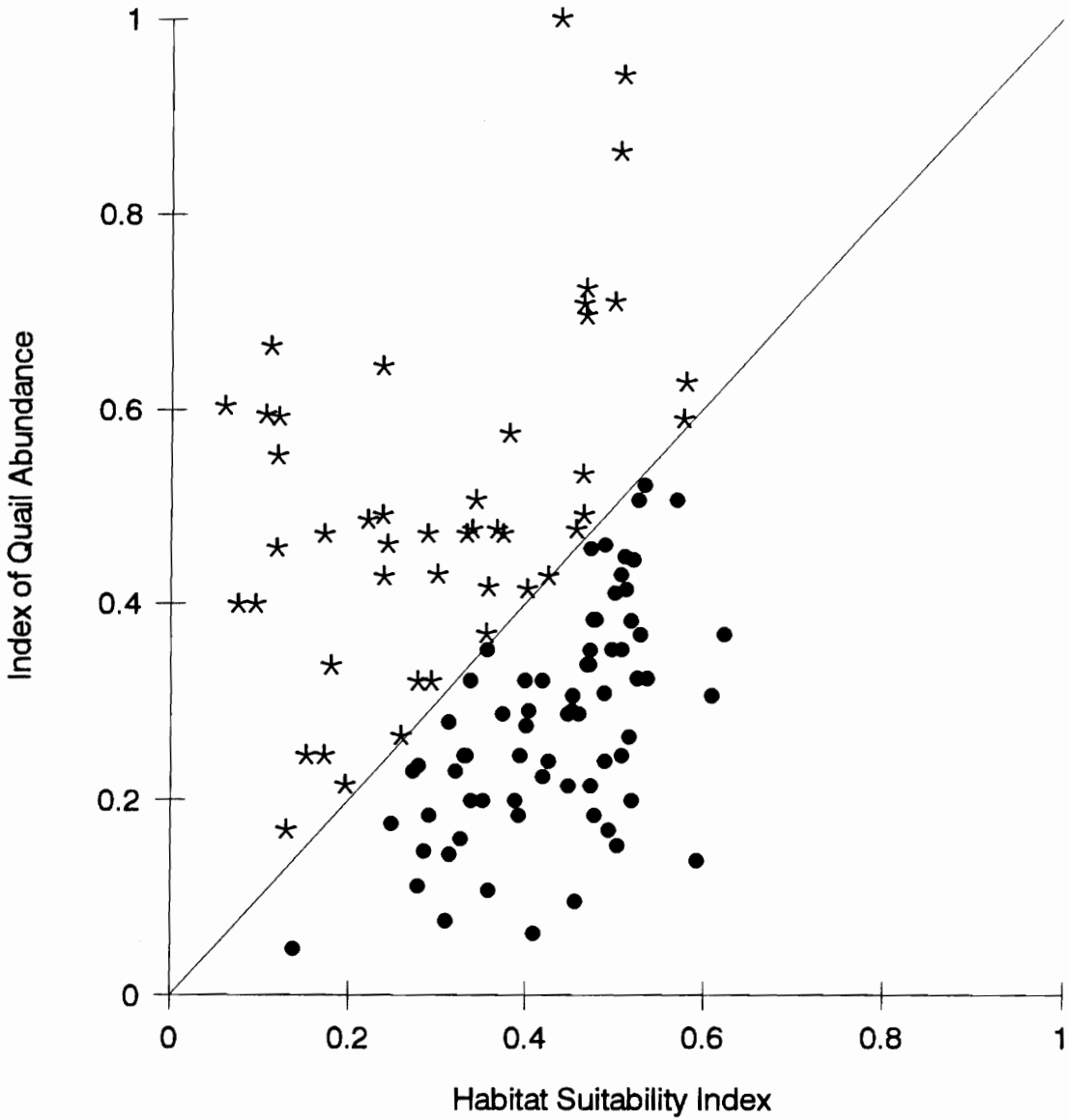


Figure 14. Relationship ($r_s = 0.10$, $P = 0.29$) between the performance measure and CRP HSI model output generated at 115 sites in Halifax County, Virginia, 1986-1991. The 45° represents a habitat-imposed upper limit to population performance. Asterisks indicate those sites where population performance exceeded levels indicated by the model. HSI model values include the interspersions of cover types.

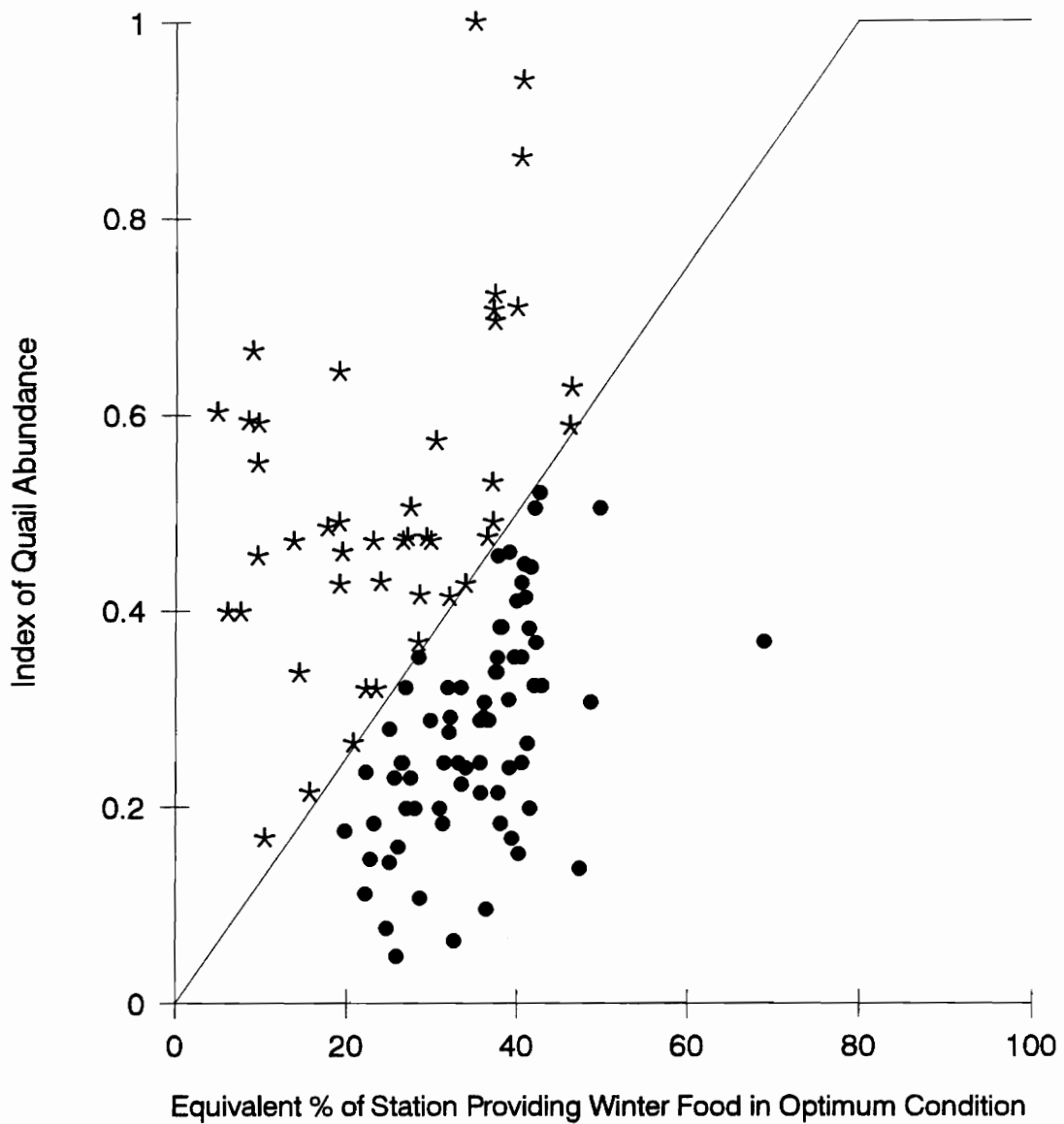


Figure 15. Relationship ($r_s = 0.08$, $P = 0.41$) between performance measure and equivalent percent of station ($n = 15$) providing winter food in optimum condition. The relative area of each polygon was adjusted to reflect the interspersed cover types. Asterisks indicate those sites where population performance exceeded levels indicated by the CRP HSI model. Sites were sampled 1986-1991, Halifax County, Virginia. The line is the SI curve for this variable (Schroeder 1985).

the performance measure.

The percent of each station affected by interspersions averaged 7.1% (SE = 0.9, n = 115). Assuming that interspersions are relevant and the relationship expressed in Figure 13 is reasonably accurate, this value is in essence an expression of the extent to which the availability of ≥ 1 of the life requisites was overestimated. An interspersions index of 10% implies that 10% of the stations were providing ≥ 1 of the life requisites at a level $<$ that initially estimated. Thus, you might expect to find relatively large values at those stations where there were fewer quail estimated than indicated by the model.

A Wilcoxon signed rank test ($S = 742.5$, $P < 0.001$, $n = 115$) on the differences between the estimates of winter food, before and after adjusting composition SIs for interspersions, suggests that "1" above may not be the case. That the results from the Wilcoxon test were significant, implies that interspersions were a relevant issue, as evidenced by the reduction in the estimate of available food. However, caution is warranted; there may be alternative explanations. First, there were relatively few large differences between estimates of available winter food, before and after adjusting for interspersions (Fig. 16). Ninety-three percent of the stations were in the 0-0.49 category. Second, if 80 m is a conservative estimate of the distance below which no adjustment in the model score is necessary, it is likely

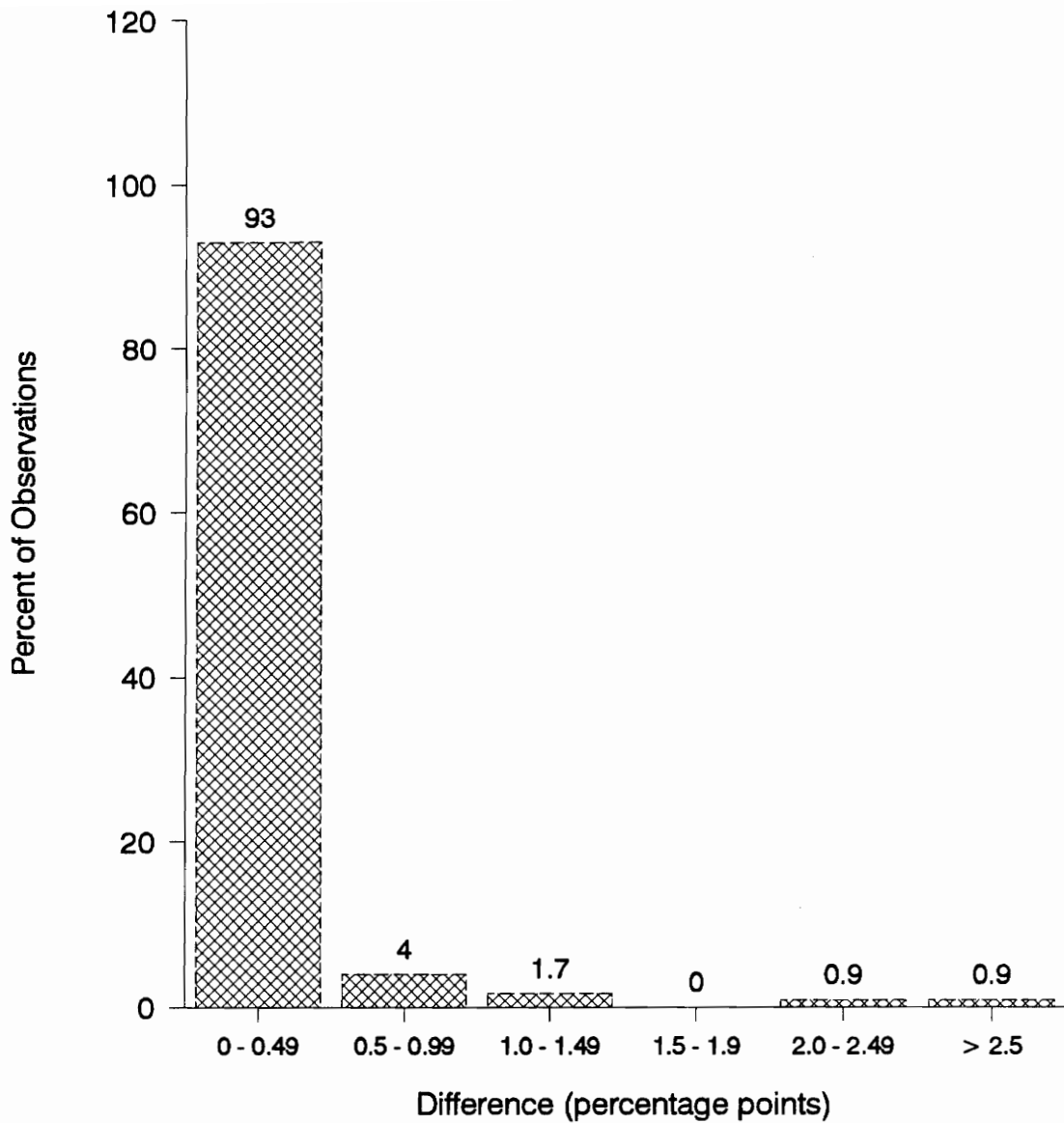
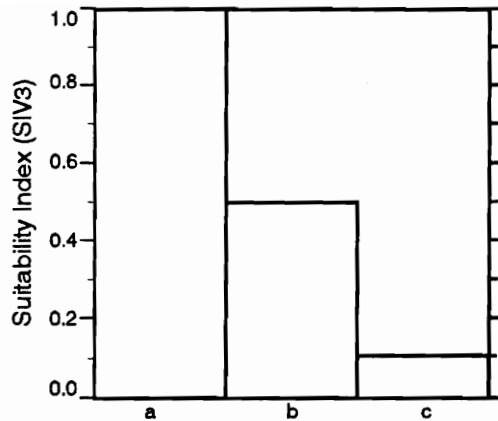


Figure 16. Distribution of differences between estimates of equivalent percent of area providing optimum winter food (OPTLWF) and the same estimate adjusted for interspersions of cover types. Data are for 115 sites sampled in 1986, Halifax County Virginia.

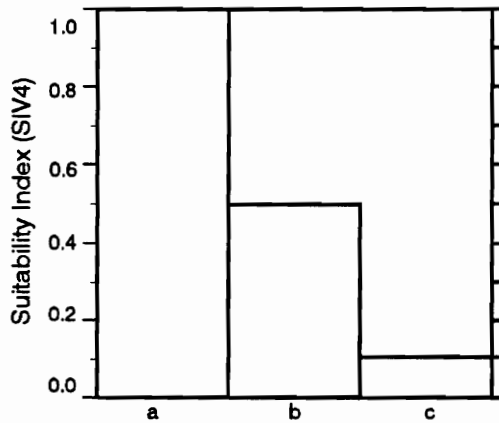
that interspersation was not even an issue. Of those stations (n= 95) with ≥ 1 polygon relative area adjusted as a result of a lack of optimum interspersation of cover types, 65% of the affected polygons at these 95 stations were adjusted by a factor of 0.8 (i.e., the missing life requisite was > 80 m but ≤ 140 m away). Thus, it seems reasonable to conclude that there was adequate interspersation of cover types on the study area and that failure to consider the role of interspersation had little to do with poor model performance.

Contribution of Crop Fields

The HSI model by Schroeder (1985) incorporates 2 variables, over-winter crop management practice and type of crop grown. These 2 variables apply only to crop fields (Fig. 17). Because crop type "a" (Fig. 17) represented, on average, approximately 3% of each station, the estimate of available winter food would decrease at all 121 stations if these 2 variables were included in the estimation of available winter food. Because I did not have precise data for over-winter crop management practice data, I assumed that all fields were fall plowed. I am confident that this is a reasonable approximation. Further reductions in the estimate of winter food would be realized if over-winter crop management practice was incorporated into the CRP HSI model.



Type of Crop:
 a) corn, soybeans, sorghum, cowpeas or peanuts
 b) other grain crops
 c) vegetable, fruit, fiber crops, or tobacco



Overwinter Crop Management:
 a) crop unharvested
 b) crop harvested, spring plowed
 c) crop harvested, fall plowed

$$LRS_i = (LRS_i + SIV3) \times SIV4^1$$

¹ See Figure 5 for a definition of LRS_i

Figure 17. Suitability indices for type of crop grown and over-winter crop management practice of the draft HSI model (Schroeder 1985).

As noted, redefining winter food to include overwinter crop management and crop type could only reduce estimates of available winter food (that is, move them to the left of their present location). Thus, in the context of improving the fit of the model, the ideal situation would be for stations where the model overestimated site quality (those below the 45° line in Fig. 10) to have significantly more crops present than those sites where population levels exceeded levels indicated by the model.

Modifying the estimate of winter food to reflect over-winter crop management and crop type grown not only failed to improve the fit of the model, it resulted in a negative relationship ($r_s = -0.19$, $P = 0.04$) between model output and the performance measure (Fig. 18). Following the modifications to the estimate of winter food, winter food was identified as the limiting factor at all but 3 of the 121 stations. The estimate of available winter food and the number of quail detected at a station were correlated negatively ($r_s = -0.25$, $P < 0.006$, Fig. 19).

An inspection of the relationship between the performance measure and cropland suggested a partial explanation for the failed attempt to improve the fit of the model via the winter food component. The 121 estimates of OPTLWF were rounded to the nearest whole number and categorized according to Table 12. Spearman correlations between the performance measure and the amount of cropland

Table 12. Correlation (r_s) between percent of station (n=121) in cropland (AREA1000) and index of quail abundance for 9 levels of equivalent % of station providing winter food in optimum condition (OPTLWF). Data were collected 1986-1991, Halifax County Virginia.

OPTLWF(%)	n	r_s	P
< 10	6	-0.06	0.91
11-15	5	0.40	0.50
16-20	7	0.21	0.64
21-25	9	0.07	0.86
26-30	22	0.43	0.05
31-35	24	0.28	0.19
36-40	25	0.43	0.03
41-45	18	0.53	0.02
>45	5	0.30	0.62

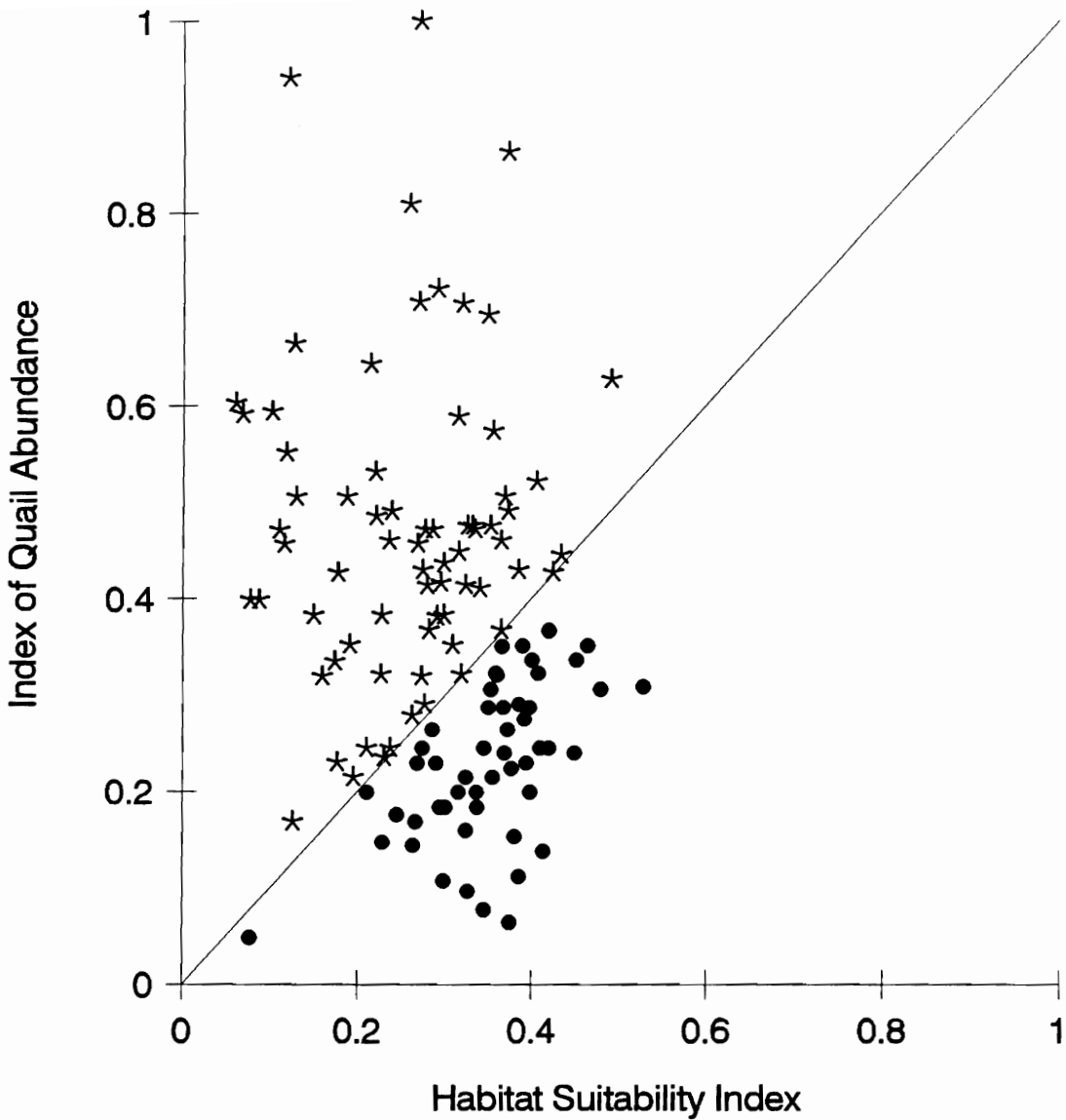


Figure 18. Relationship ($r_s = -0.19$, $P = 0.04$) between the performance measure and CRP HSI model output generated at 121 sites in Halifax County, Virginia, 1986-1991. The 45° represents a habitat-imposed upper limit to population performance. Asterisks indicate those sites where population performance exceeded levels indicated by the model. The winter food component of the HSI model developed by Schroeder (1985) was used instead of the CRP model to evaluate habitat conditions.

at a station were computed for each of the 9 levels of winter food.

The number of observations per category ranged from 5 to 25 (Table 12). Correlations for 3 of the 9 categories were significant ($P < 0.05$) and positive (Table 12). Correlations ranged from 0.43 to 0.53. Although nonsignificant, correlations for all of the other classes but 1, were positive. Thus, for a relatively constant level of winter food, those sites with the greatest amount of crops generally had more quail. This relationship helps to explain the negative relationship between model output and the performance measure after redefining winter food.

As a result of modifying the estimate of winter food, those sites above the 45° line in Figure 10, were shifted further to the left of their present location than those below the line. Moreover, the further they were above the line, the more they moved to the left. This action was a consequence of the fact that, since those sites above the line had more quail than those below, and thus generally more crops, they were affected most by redefining winter food. Again, the more crops at a station, the greater the reduction in OPTLWF. Additionally, although the points falling below the 45° line would be moved some in the appropriate direction (i.e., to the left of their present location) by the proposed changes, those sites positioned closest to the line will be moved relatively more than those sites furthest from the line because they have relatively more crops. This however, is opposite the

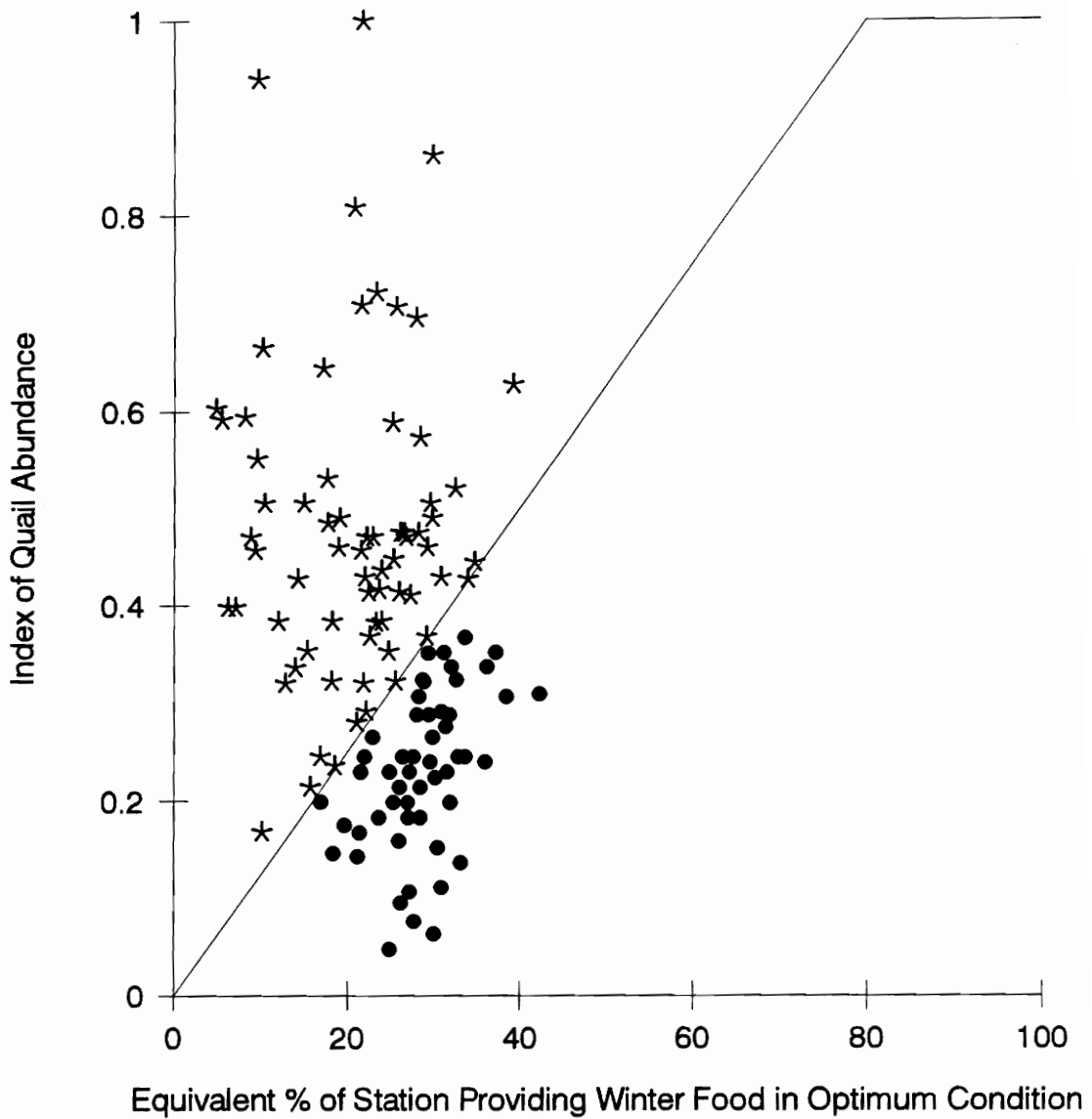


Figure 19. Relationship ($r_s = -0.25$, $P < 0.006$) between the performance measure and equivalent percent of the station providing winter food in optimum condition. Asterisks indicate those sites where population performance exceeded levels indicated by the model. The winter food component of the HSI model developed by Schroeder (1985) was used in place of the CRP HSI model to evaluate habitat conditions. The solid line is the SI curve for this variable.

desired effect of the action. Figure 20 illustrates the ideal and observed response of the distributions of points in Figure 10 to the proposed changes in the estimate of OPTLWF.

Individual Variable Suitability Indices

There are 3 possible reasons why I detected no relationship between winter food and the performance measure. First, as previously proposed, a life requisite other than winter food may have been limiting quail populations at the time of sampling. Second, the variables used to describe winter food may be providing a poor estimate of actual winter food resources. Third, the individual variable SI curves may have incorrectly assigned habitat quality. If we assume, at least temporarily, that the first is not the case, it should be possible to evaluate the validity of the latter 2 by plotting the performance measure against estimates of habitat suitability indicated by the model (i.e. each variable).

Means for each of the variables were computed for each of the 121 stations by averaging over all polygons within the station. The size of the polygon was used as a weight. If the variable is an indicator of winter food resources, a relationship between these weighted means and the performance measure is expected. Furthermore, if the model SI curve is reasonably accurate, one also would expect

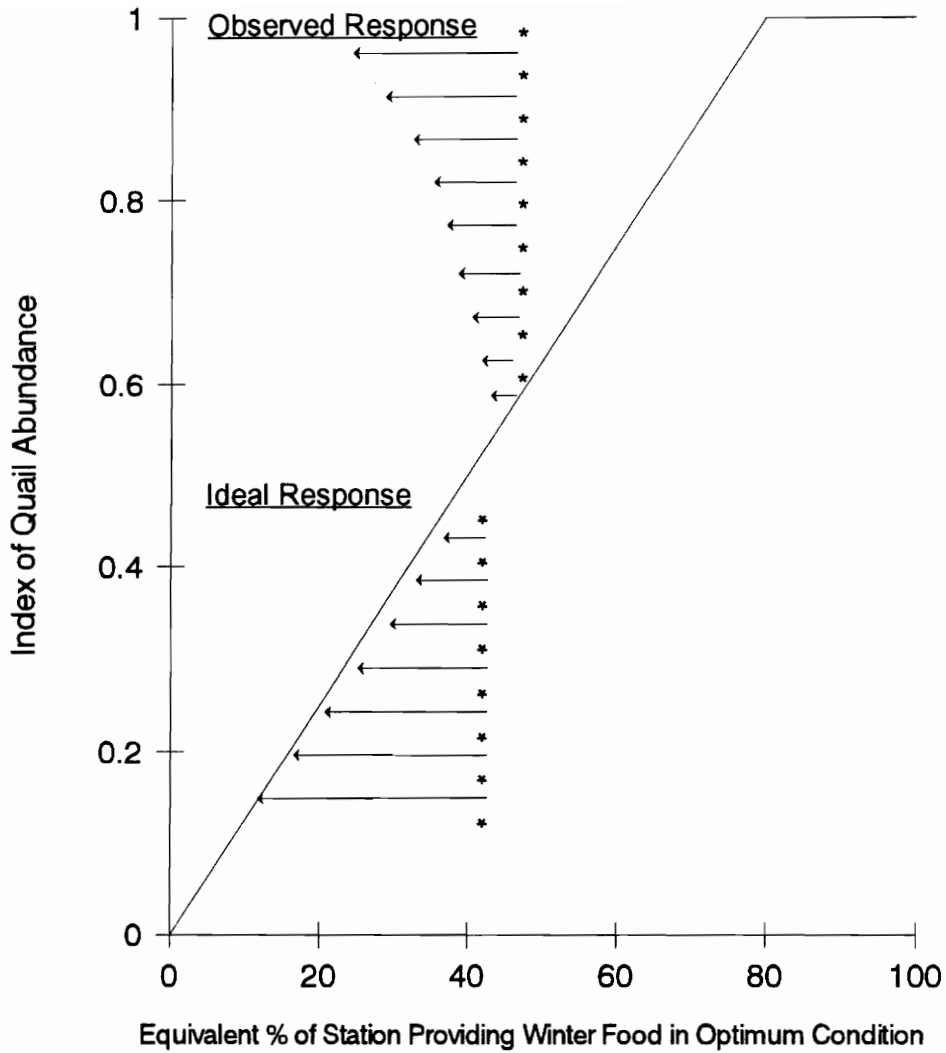


Figure 20. Schematic diagram indicating ideal and observed responses of the distribution of points about the line relating equivalent % of station providing winter food in optimum condition and the performance measure after adjusting the winter food LRSI to reflect over-winter crop management practice and crop type present. The proposed changes affect only crop fields.

this distribution of points to be comparable to the hypothesized relationship expressed in the model, i.e., the SI curve.

It is evident that changes in the individual variable suitability index curves would do little towards improving the fit of the model (Figs. 21, 22, 23). From an inspection of Figure 21, the data suggest that the curve for percent canopy cover of herbaceous quail foods should be shifted to the left of its present location. This would increase the SI values for nearly all the sites, resulting in an increase in the SI value for OPTLWF, assuming the curves for the other variables were unchanged. By increasing model scores, a larger percentage of the 121 sites would fall under the 45° line in Figure 10. However, because there is so little variation among the 121 sites for percent canopy cover of herbaceous quail foods, changing the curve would affect nearly all the stations equally. As for percent bare or lightly-littered ground (Fig. 22), the present SI curve appears to be reasonable. Finally, although the distribution of the data suggests that the SI curve for density of mast producing trees should be redrawn (Fig. 23), the changes would have no effect on model fit since nearly all stations would have the same value for this variable.

Limits of Habitat Models

Is a model of northern bobwhite habitat possible? Although it is not

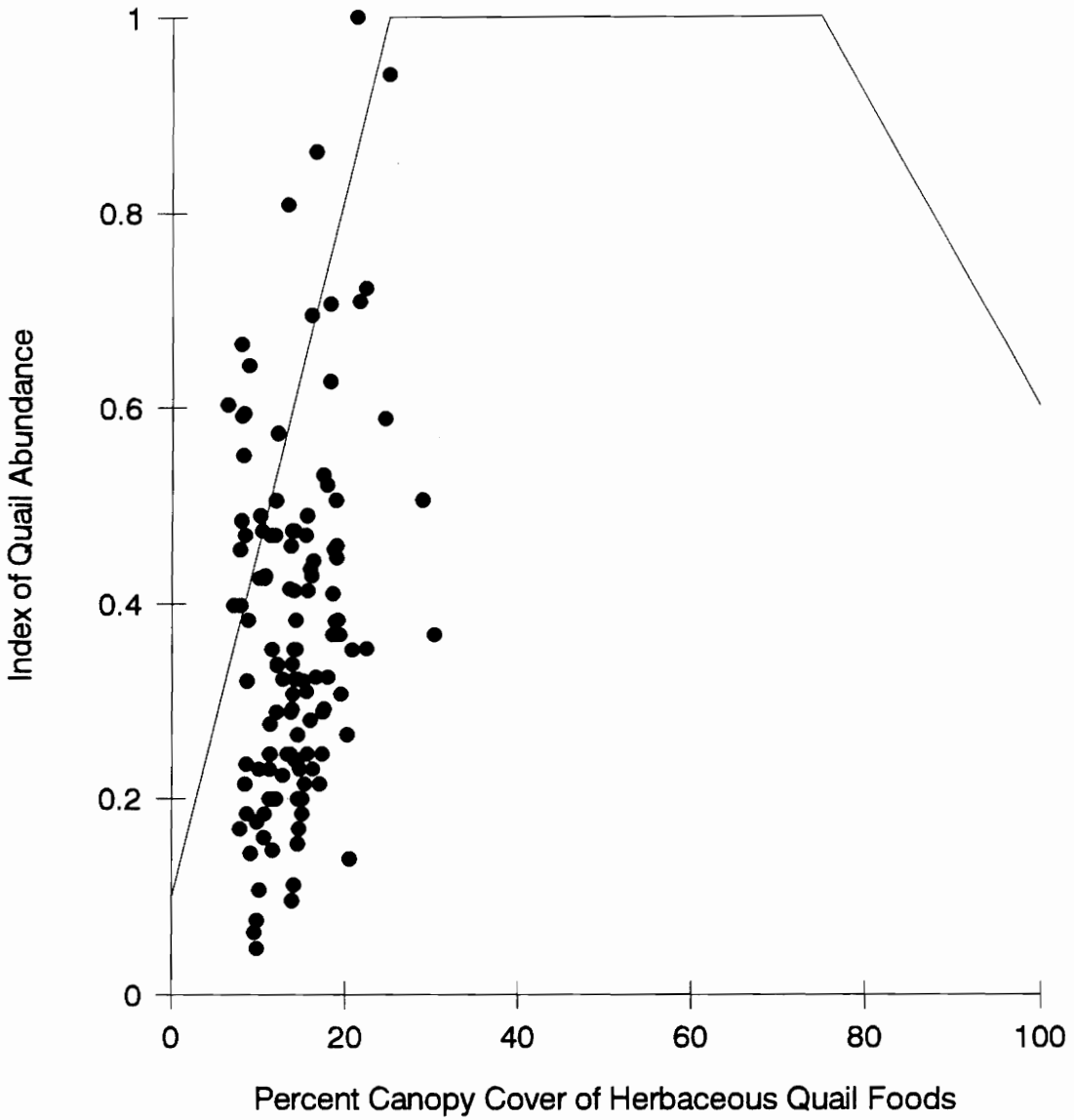


Figure 21. Relationship between performance measure and the percent canopy cover of herbaceous quail foods for 121 sites sampled 1986-1991, Halifax County, Virginia. The solid represents the hypothesized relationship between habitat suitability and percent canopy cover of herbaceous quail foods from the HSI model (Schroeder, 1985).

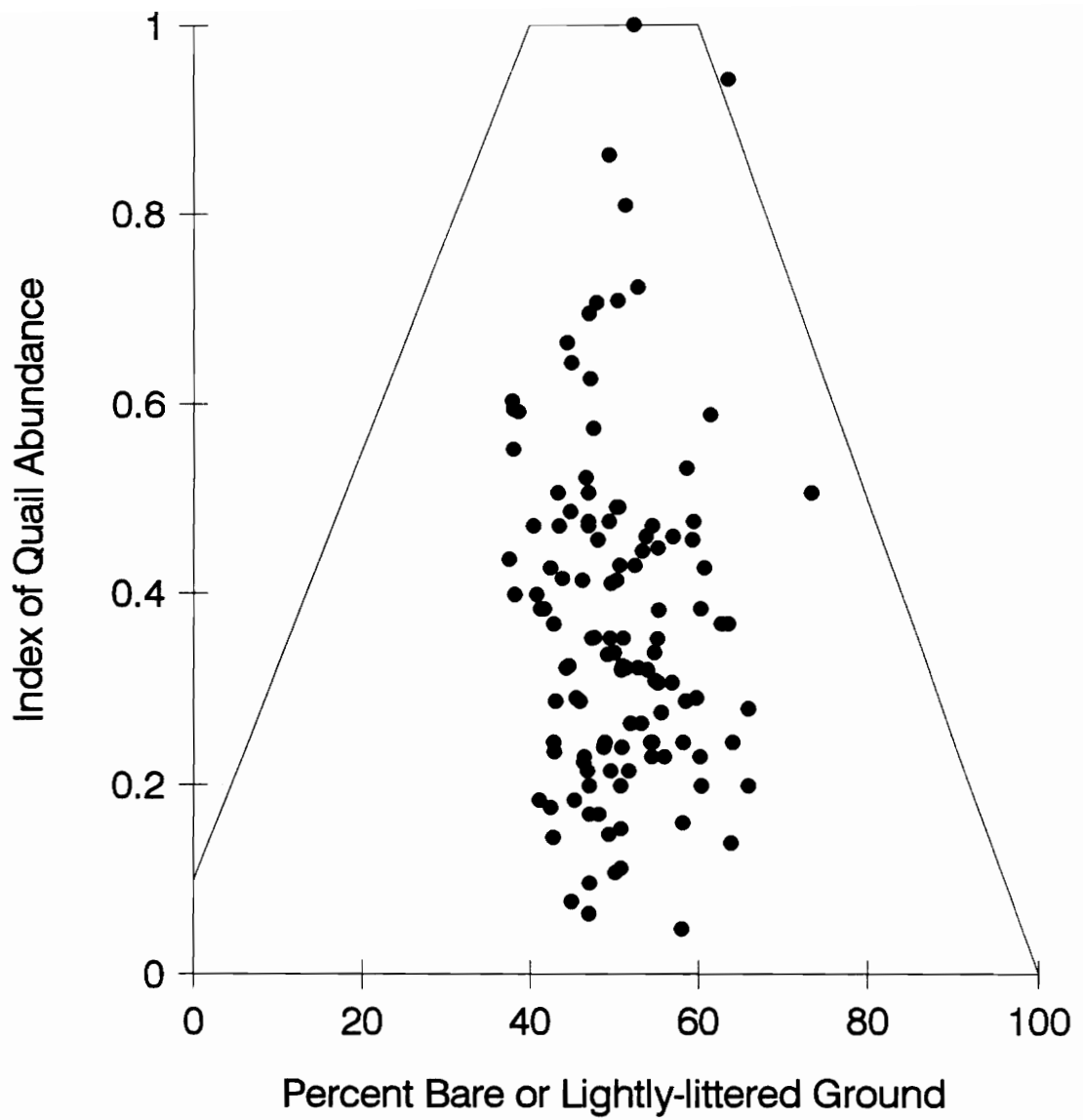
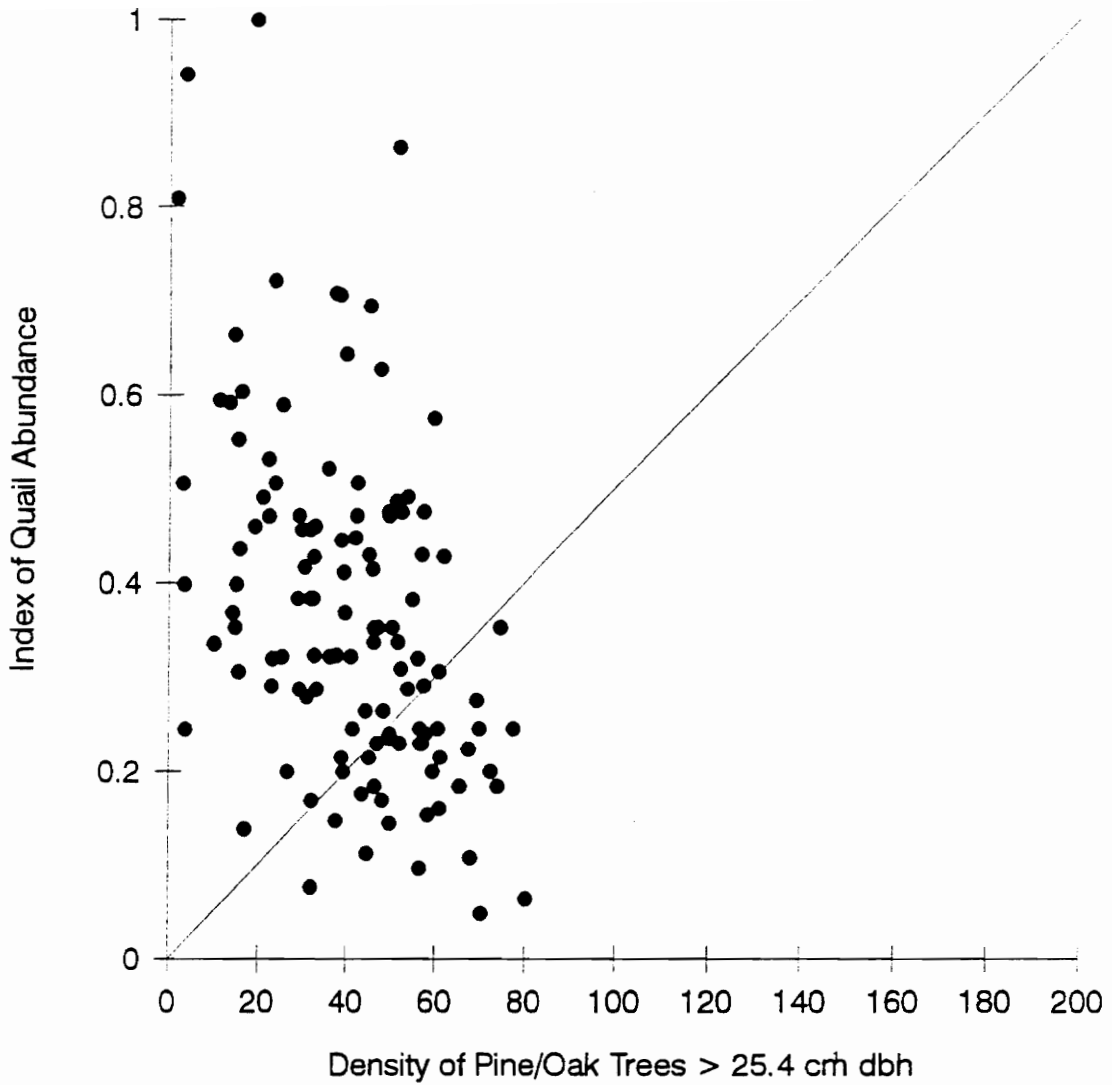


Figure 22. Relationship between performance measure and the percent bare or lightly-littered ground for 121 sites sampled 1986-1991, Halifax County, Virginia. The solid line represents the hypothesized relationship between habitat suitability and percent bare or lightly-littered ground from the HSI model (Schroeder 1985).



This is a generalized curve. The slope of the curve will vary with the mean dbh of trees > 25.4 cm dbh.
See Figure 2.

Figure 23. Relationship between performance measure and the density of pine and oak trees ≥ 25.4 cm dbh for 121 sites sampled 1986-1991, Halifax County, Virginia. Mast is considered a significant food source when available. The solid line represents the hypothesized relationship between habitat suitability and mast availability from the HSI model (Schroeder 1985).

guaranteed, ecological theory at least provides the framework within which such modeling attempts are justified. Hilden (1965) described the process of habitat selection in birds in terms of ultimate and proximate biological factors. Ultimate factors, he proposed, were necessary for a species' survival and reproduction and as such represented the underlying reason why species select to breed only in certain habitats. Proximate factors on the other hand, may or may not have any biological significance. Their role, he argued, was simply to elicit a settling response from the species. Those individuals responding to such stimuli would be favored and preference for those habitats eliciting such a response would evolve. More directly, preferences and qualities of such environments would coevolve (Orians and Wittenberger 1991). There are dimensions of the environment to which a species must respond if it is to successfully reproduce. This basic premise of ecological theory has been the catalyst behind attempts to develop models of species-habitat relationships and, aside from experimental and study design, the success of such models is largely determined by our ability to identify those cues that the animal receives from the habitat that are associated with probabilities of survival and reproductive success (Noon 1986).

According to Morris (1987:269), "Habitat determines the availability of resources, refugia, nest sites and mates; the abundance of conspecifics and

interspecific competitors; the risk of predation, parasitism, and disease; and a host of other factors that influence reproductive success." From this, it is tempting to infer that an evaluation of habitat should provide some measure of reproductive success or some other measure of population performance. Predictive habitat models should be possible. Clearly, this is not always the case, the principal reason being that the physical features of the environment, those around which we structure our model, simply define the upper and lower limits within which factors such as disease, predators, and competitors may operate. As a result, there is a limit to the predictive ability of the physical habitat. Moreover, these general descriptions of habitat may represent only correlative factors. If these factors are not consistently linked with the causative factors, the model will ultimately fail (O'Neil and Carey 1986). They stated that sometimes even the best designed studies, "...with well defined objectives, experimental designs appropriate to the objectives, sampling plans that meet statistical and mathematical assumptions, methods that estimate accurately and without bias and wise analysis of data will fail (O'Neil and Carey 1986:207)." Moreover, some species are simply poor candidates for habitat models.

Despite nearly 50 years of "research," my review of 3 reviews (Schroeder 1985, Dimmick 1992, O'Neil 1993) of northern bobwhite habitat needs revealed a limited number of studies that provide any empirical quantitative evidence for a

population-based model of northern bobwhite habitat. Work by Shultz and Brooks (1958) represents 1 of the first attempts to quantitatively describe the relationships between northern bobwhite population levels and land use characteristics. The authors developed a multiple regression model relating farm composition and bobwhite population levels. Models were developed for 3 farming types. Their final models, which included amount of pasture, croplands, and woodlands, were able to account for 29, 57 and 70% of the variation in numbers of coveys reported. The Missouri Department of Conservation has developed a series of Wildlife Habitat Appraisal Guides (WHAG), including 1 for the northern bobwhite. These guides, developed from earlier attempts to model the respective species habitat relationships, are based on the same premise as HSI models - that wildlife habitat can be numerically described by a habitat suitability index (Urich et al. 1984). Although the authors stated that the guides were subjectively verified, I am not aware of any attempts to validate the northern bobwhite WHAG. An appraisal guide also has been developed for Oklahoma (Bidwell et al. 1991). An index of interspersions was developed by Baxter and Wolfe (1972) for quail in Nebraska. Later, Priddy (1976) reported a positive correlation between an index of relative abundance based on call count data and this interspersions index. Although several other indices of interspersions have been developed and suggested for use in the analysis of bobwhite

habitat, I am not aware of any other applications.

Other attempts to model the species' habitat needs have been extremely limited. Cline (1988) reviewed most of the extant literature on northern bobwhite habitat relationships and found only 3 attempts to model this species' habitat requirements. Aside from the HSI model developed by Schroeder (1985), he reported that Baxter and Wolfe's (1972) index and an overly simplistic attempt by Urich et al. (1983) were the only other models of northern bobwhite habitat. In the late 70s, an effort by researchers at Texas A&M University (Reid et al. 1977) revealed that spring whistle counts were correlated with habitat parameters that the authors assumed were associated with food, cover, nest sites and song posts. These assumptions were based on opinion and previously published work. Later, Cline et al. (1991) developed a multiple regression model of northern bobwhite summer habitat use that accounted for just under 45% of the variation in relative quail densities across 121 sites in Virginia using a series of land use variables. Predictors in the final model included the area of fallow fields and other miscellaneous cover types, mown lawns and 3 variables describing dense, woody canopies. Brady et al. (1993) examined relationships between land use characteristics and bobwhite population levels in Kansas. Their results indicated that 16 land use variables, 3 soil variables, and 1 spatial variable were significantly different in counties where

bobwhite were present from counties where they were absent. Moreover, they reported that 16 land use variables, 5 soil variables and 3 spatial variables distinguished between counties where bobwhite abundance was classified as high or low. Roseberry and Richards (1992) developed a large-scale model of northern bobwhite habitat that utilized remotely-sensed land use data. They later used this model in an evaluation of the potential impacts of the Conservation Reserve Program on northern bobwhite habitat in Illinois (Roseberry et al. 1994). The model was structurally similar to the HSI model for the northern bobwhite (Schroeder 1985). To the best of my knowledge, the validity of the model by Roseberry et al. has never been established. More recently, Rice et al. (1993) developed and tested a habitat model for predicting autumn population densities of northern bobwhites on subtropical, semiarid rangelands in Texas. Habitat assessment considered food availability (forb coverage and bare ground) the extent of thermal cover (canopy cover of woody plants) and the proportion of sand-sized particles in the soil. As a means of incorporating the effects of history at each evaluation site, the authors included an index of precipitation, which they assumed was a correlate of quail density. They found that precipitation was a stronger predictor of bobwhite density than their habitat model. A substantial portion of the variation observed in density was unexplained by the model.

That these attempts to "model" northern bobwhite habitat were at best, moderately successful, may suggest that, despite the opinion of O'Neil (1993:17), the bobwhite is not a good candidate for an HSI model. The northern bobwhite is a habitat generalist with a potentially high reproductive output that occupies a patchy environment that is relatively temporally unpredictable. Van Horne (1983) argued that r-selected species, such as the northern bobwhite, are especially troublesome when it comes to developing predictive habitat models. As Flather and Hoekstra (1989) pointed out, the opportunistic strategy and variable population characteristics of r-selected organisms suggest that these species tend to be independent of the upper resource limits of a particular habitat. It is possible that species of this nature are not habitat limited once some minimal conditions have been met. Given this, and the fact that bobwhite population levels are greatly influenced by density independent factors, most notably weather (Rice et al. 1993), it is possible that an accurate predictive habitat model is not likely or will require either a more extensive or intensive approach than used in the development of the HSI model.

Density: An Index of Habitat Quality?

The use of density data as the performance measure may have contributed to the failure of the model. I considered this reasonable because 1) it is assumed that

HSI models are linearly related to carrying capacity and 2) there is some evidence to suggest that density data, as used in the present investigation, may provide misleading information about the carrying capacity of a site. Thus, while the output from the model does provide an index of carrying capacity of the site, the number of calling males as an index of density, might not.

Habitat features are necessary but not sufficient to determine population size or distribution. Prediction aside, habitat does effectively determine the upper limit or potential of a population in a given area. This potential is often referred to as the carrying capacity of the site, an ecosystem-imposed upper limit on population size. According to Fretwell and Lucas (1969) all habitats have a basic suitability, which is an expression of the site's potential contribution to the gene pool of the population. Among other things, this potential is a function of the availability of resources that provide the animal's basic life requisites that allow it to survive and successfully reproduce. It is assumed that these resources, or surrogate measures thereof, can be identified and with the use of measures of population performance, predictive models of habitat potential can be developed. HSI models are presumably such models. They do not purport to be predictors of actual population levels but rather habitat quality (Bart et al. 1984), which has been defined by Maurer (1986:556) as "the suitability of an area to support a reproducing population of a given species or

group of species." HSI models provide an index of **potential** population performance (carrying capacity), insofar as density and other population characteristics can be used to define this potential. If habitat does in fact establish an upper limit, and those variables that ultimately set such a limit have been correctly identified, output from an HSI model should be related to the carrying capacity of the site.

Conceptually, HSI models might be considered operational versions of the Fretwell-Lucas model (1969) of habitat selection under the assumption of an "ideal free distribution," for the simple reason that both assume that nonlinearities in habitat-density relationships are absent (O'Connor 1986). Thus, density or some index thereof, can be used as a measure of habitat quality, i.e. carrying capacity, across the entire range of possible habitat conditions that the species might occupy. The basic premise of the Fretwell-Lucas model is that presumably animals are capable of evaluating a habitat's relative suitability, which is its basic suitability adjusted for the density of individuals already occupying the site. Further, it assumes that if they have free access ("ideal free") to all available habitats, then the density of individuals in that habitat should be a reflection of the basic suitability of the habitat. In other words, despite a density dependent depression of reproductive fitness, the reduction is constant across all habitats. The relatively better habitats

support more individuals than those of lower quality. However, the fitness of these individuals is assumed to be equal to those in marginal habitats, where presumably fewer individuals are resident. Judging from the extent of research on species habitat relationships that have employed density and density indices, it would appear that "nonlinearities in habitat-density relationships are nonexistent" is one of those "principles of wildlife management." Limited research suggests otherwise.

Van Horne (1983) provided probably the first indication that under some circumstances involving certain species, density-habitat relationships may be suspect. Using empirical data derived from her research on Peromyscus maniculatus, she was able to show that despite the fact that high-density adult habitat was also high quality (based on male body weight and adult overwinter survival) habitat, high density subadult habitat was low quality. She provided other examples from the literature and suggested that a decoupling of the density-quality relationship is likely in seasonal habitats and temporally unpredictable environments. Species with a life history strategy that would allow for opportunistic increases when unusually favorable conditions exist are likely to pose problems. Species with marked social dominance traits where limits to compression of territory size (O'Connor 1985 in O'Connor 1986) 1986), for instance, may force individuals from higher quality habitats into marginal areas. As non-breeding individuals accumulate in these areas,

an inverse relationship begins to develop between reproductive success and density. Other factors such as the possibility of a time lag in a species' response to resource availability (Bart et al. 1984), of which site tenacity might be a special case (O'Connor 1985, in O'Connor 1986), and the effects of overall population density on a species distribution among habitat types should be considered as potential threats to the assumed linear relationship between density and quality. Efforts by researchers in England (O'Connor 1986) and Poland (Diehl 1986) convincingly demonstrated that inferences about habitat relationships of songbirds varied with population levels. O'Connor (1986) pointed out that only when populations were low would it be appropriate to base estimates of habitat quality on density. More recently, Hobbs and Hanley (1990) suggested that, in environments where there are few high quality resources and an abundance of lower quality resources, and resource quality and quantity are not substitutable, that inferences about carrying capacity based on resource use/availability data may be wrong when populations are not at carrying capacity.

Despite numerous references to VanHorne's (1983) paper, which has been discounted as a special case (Fagan 1988) , there are far more proposed hypothetical scenarios where this uncoupling may occur than there are experimental data sets to support its existence. Population density, especially from long-term data, should

provide some measure of habitat quality. Perhaps the best measure of carrying capacity would be mean population density from estimates conducted regularly over several generations (Bain and Robinson 1988). Gaud et al. (1986) suggest that in developing predictive habitat models from density data researchers should collect such data over a long enough span so as to capture the natural variation in the population being studied. Their work suggests that 5 years from ≥ 3 sites should be adequate. The literature is replete with warnings against using point in time data [e.g. Pajak and Neves (1987)] and its shortcomings. The 6 years of density data used in the present investigation notwithstanding, there still is some doubt that even long-term data might provide reliable estimates of habitat quality because of the possibility that sink populations may be being maintained by sources external to the population, i.e., emigration (Pulliam 1986). Given the above discussion, it is compelling to offer the use of density data as a performance measure as a partial explanation for the failure of the model. I doubt, however, that the spring call count data contributed to model failure, at least for reasons mentioned above.

It is assumed that output from the northern bobwhite HSI model is an index of carrying capacity. However, the index is only a measure of carrying capacity insofar as the data used to construct the model are such an index as well. Because the majority of the data used to construct the model was likely short-term

population-based data, the HSI model is only an index of carrying capacity if such data are also an index of carrying capacity. Consequently, the observed lack of model fit has little to do with using density data to validate a model, which, it turns out is based on density data.

Were the Data Appropriate for the Test?

The present model was based on literature and the opinions of 9 individuals assumed to be experts (O'Neil 1993). If data defined the extremes of each of the SI curves, and opinion was used to connect the data points, then it is not unreasonable to question the accuracy of some or all of the curves. The author of the model designed it for use in evaluating the species' response to extreme environmental perturbations such as complete or near complete habitat destruction. As a result, it would be logical to construct a model with data that covers such extremes. It may have been that the range of conditions on my study area did not begin to approach those that the model was designed to detect. In other words, differences detected among the stations on my study area may not have been measurable at the scale used in the construction of the model. I recognize that such a hypothesis seems at variance with the apparent precision presented by the Suitability Index curves throughout the model. However, if these curves are based on more opinion than

data, then it is possible that such precision is misleading and that actually a step function would be more appropriate in many cases. The entire range of conditions represented on my study area may have resided in a single step.

Study Design

O'Neil (1993) suggested that the results of a model test are a function of 4 factors, 1 of which is the data on habitat features used to test the model. She noted that data used to run the model must be collected to match the author's definitions. The problem in many cases however, is that definitions are often vague or lacking. In 1984, participants of a workshop on fish HSI models concluded that 1 of the primary barriers to successfully applying such models is the lack of precise definitions for variables. They proposed that a glossary of terms should be included in each model as well as instructions on how each variable should be measured (Terrell 1984). Li et al. (1984) suggested that the use of multiple data sources and differences in definitions of variables associated with such data sets may have contributed to the lack of correlation between observed and predicted HSI values for the cutthroat trout (Salmo clarki clarki) and Coho salmon (Oncorhynchus kisutch) models they tested. Similar problems may have contributed to poor model performance in the present investigation in either of 2 ways. First, since we

employed a cover typing system that differed from that included with the HSI model, it is possible that portions of the study area were excluded from consideration because we erred in the conversion of our cover classification system to the system used in the model. Secondly, it is possible that I failed to correctly identify locally important quail foods.

As noted previously, the HSI model for the northern bobwhite is a multiple cover type-based model in that the user is instructed as to which cover types should be evaluated for their potential to provide each of the 3 life requisites. As a result, the development of a cover type map is 1 of the first steps in the application of the model. Because the present investigation began not as a test of the HSI model but instead as a survey of the relationships between primary land uses and quail population levels on agricultural lands , the cover typing system employed was adopted from researchers in Michigan (Cline pers. comm). As a result, to apply the present model, it was first necessary to determine how each of the approximately 4,500 polygons on my study area would have been classified had the U.S. Fish and Wildlife Service's protocol been used initially. In many cases, there was very little uncertainty, such as in the case of crop fields. However, with forested habitats, in many cases there were no obvious matches between the 2 systems. This mismatching may have resulted in the exclusion of habitats that were actually contributing to

observed population levels and ultimately to poor model performance.

Because the winter food component of the model was responsible for model scores at 115 of the 121 sites, it is not unreasonable to suspect that failure may have at least partially been attributable to discrepancies between assumed sources of winter food and those actually consumed. In the present investigation, I used Landers and Johnson's (1976) comprehensive review of 27 bobwhite food habits studies representing over 20,000 birds collected throughout the southeastern United States to identify candidate sources of food for the species on the study area. This review identified major food sources by physiographic province, of which the Piedmont seemed the most appropriate for use in the present investigation. I considered 45 species (Appendix Table 2). Without a food habits analysis from the study area or ≥ 1 from the region, it is difficult to know for sure whether a locally important food source was missing from the list used in the present investigation. Given the comprehensive nature of the study used to produce the list used in the present study and the lack of any substantive reason to believe my study area is unique to the Southeast Piedmont, I have little reason to believe that a failure to identify local food sources was a major contributor to model failure.

Another possible factor associated with the winter food component of the model that may have contributed to the neutral results could be a discrepancy

between foods assumed to comprise the early spring diet and those actually consumed. Of concern is the fact that nearly all of the food habits studies are based on fall-collected birds, primarily those killed during the hunting season. Like nearly all nonmigratory animals, the quail faces its biggest challenges to survival during the late-spring. Thus, if the species shifts its diet to "nontraditional" quail foods during this period, and the availability of these foodstuffs is not positively correlated with the availability of fall-winter foods, then you would expect to find no relationship between the number of calling males and the availability of traditional food sources.

Scale Problems

"Landscape ecology cannot escape dealing with spatial analysis, spatial scale, and scale-change effects (Meentemeyer and Box 1987)." Scale cannot be ignored in the analysis of wildlife-habitat relationships. Failure to consider scale can result in inconclusive, misleading, and unexpected or contradictory results (Best and Stauffer 1986). Every population will exhibit variability on a range of scales. Conceivably, different ecological processes can create and maintain this variability (Levin 1992, Downes et al. 1993). As a result, the scale of the investigation is likely to determine the patterns that one finds (Blenden et al. 1986, Hamel et al. 1986, Larson and Bock 1986, Laymon and Barret 1986, Rotenberry 1986, Morris 1987, Pajak and Neves

1987, Wiens 1989, Menge and Olson 1991, Orians and Wittenberger 1991, Bowers and Dooley 1993, Downes et al. 1993, Gibson et al. 1993, Reed et al. 1993, Crist and Wiens 1994, Powell 1994) or fails to find. Moreover, as the spatial scale increases, so does the time scale of important processes, simply because the processes tend to operate at slower rates (Wiens 1989). Below, I consider the role that scale may have played in the present test of the northern bobwhite HSI model. I begin by considering the potential effects of study area size on study results. Secondly, I present evidence that patterns of species-habitat associations are scale-dependent and consider the implications of disparity in scales between data used to develop the model and those used in the present test of the northern bobwhite HSI model. Finally, Van Horne and Wiens (1991) emphasized the importance of testing a model under conditions comparable to those under which the model was developed. I propose that, consistency among scales used to test and develop the model notwithstanding, because habitat conditions on most of today's farms are different from those from which data was gathered in the development of the model, the model may no longer be entirely valid.

Study area size should not be an arbitrary decision. In the case of resource management, it should reflect the scale at which the management action is likely to occur. If our interest is in variation in population density, then the study area needs

to be sufficiently large to obtain reliable population estimates (Morris 1987). Factors such as mean home range size, habitat heterogeneity, and the degree of habitat specialization by the animal are other factors to consider (Laymon and Barret 1986). Larger study areas reduce the likelihood of sampling error and the effects of individual idiosyncracies (Wiens et al. 1986). However, increases in study area size usually come at the expense of a loss of detail of micro-habitat conditions (Morris 1987).

The size of the study area will influence the patterns one will likely detect (Levin 1992) and is an essential consideration in model validation (Blendon et al. 1986). Wiens (1986) proposed that plot size contributed to a lack of association between shrubsteppe bird species and their habitat when these associations were considered at a local scale. Pajak and Neves (1987) reported finding no relationship between HSI model output and standing stock estimates when the sample unit was 50 m stream section. However, when they increased the grain (plot) size they found standing stock and model output to be highly correlated. They believed that annual fish movements of up to 400 m, homogeneous habitat, and improper variables contributed to the lack of correlation when 50 m sections were used. Because species respond to factors operating at different scales, appropriate study area size varies with species (Downes et al. 1993).

Data summarized by Bidwell et al. (1991) indicated that the home range of the northern bobwhite rarely exceeds 33 ha and most commonly ranges between 8 and 16 ha. They noted that, while rare, it is possible that < 2 ha of land may meet the bobwhite's year-round habitat needs. Dimmick (1992) reported that the average home range size generally ranges from between 5 and 40 ha and that actual size depends heavily on the quality of the habitat. On lands managed intensively for northern bobwhites, the mean home range size has been reported as 15 ha (Bidwell et al. 1991). Wiseman and Lewis (1981) reported a mean home range size of 4.4 ha (SE = 0.6 ha) for 8 coveys. Estimates were based on radio telemetry data collected during the fall, winter, and spring. Saunders (1973) estimated the mean home range size of unmated male bobwhites during the breeding season to be < 7 ha. These data were collected on farms intensively managed for northern bobwhite in western Tennessee.

The HSI model for the northern bobwhite purports to evaluate year-round habitat quality. Consequently, plot size used in an evaluation of the model must be at least as large as the annual range of the species. In the present investigation, estimates of quail abundance were generated at 121, 400-m radius circular plots (~54 ha). As noted previously, this plot size was selected because under normal conditions, it is unlikely that a whistling male bobwhite will be detected beyond 400

m. Given the average home range size data reported above, it is highly likely that each of my study sites were not only large enough to provide the species year-round needs, but that each could contain ≥ 2 home ranges. Furthermore, it is unlikely, given the extent (size) of the study area, that geographic location could have differentially overridden the effects of habitat on quail population size and subsequently contributed to the disparity between observed levels of abundance and those indicated by the model. Researchers in Indiana (Backs et al. 1981) and Tennessee (O'Neil 1993) used study sites that were comparable in size to mine; both recorded significant relationships between northern bobwhite density and various habitat measures. In conclusion, I do not believe that plot size nor study area size contributed significantly to the absence of a relationship between model output and the performance measure.

The scale of the investigation is likely to have dramatic effects on the patterns that one finds (Wiens 1989). For instance, when the relationship between the least flycatcher (*Empidonax minimus*) and American redstart (*Setophaga ruticilla*) are examined at the scale of 4 ha plots, the distributions of these species are correlated negatively. However, at the regional scale, the species are associated positively with one another. Work by Orians and Wittenberger (1991) revealed that, while odonate emergence was a significant predictor of settling rates by yellow-

headed blackbirds (Xanthocephalus xanthocephalus) at the pond scale, odonate emergence varied independently of nest densities within any given pond. A similar scale dependence was noted by Powell (1994), who examined habitat selection by fishers (Martes pennanti) in Ottawa National forest, Michigan. The author's work suggested that fishers selected habitat at ≥ 2 scales and factors responsible for their distribution at each of these scales were different. Hamel et al. (1986) reported that predictions of avian community composition were scale dependent. At relatively large scales, predictable associations should occur. However, at more local scales these relationships tend to become submerged (Rotenberry 1986).

Much of the unpredictability at the fine-grained spatial scales is attributable to a stochastic phenomenon (Levin 1992). A large percentage of this variation is due to the interaction of physical and biotic factors, which at the larger scales appear to be dominated more by climatic features (Menge and Olson 1991, Wiens 1989). In essence, the effects of local heterogeneity are "averaged out" at larger scales (Wiens 1989). Reed et al. (1993) suggested that plant-plant interactions are important at small scales but that the physical environment dominates at larger scales. They proposed that the correlation between vegetational composition and environment increases with increasing grain (plot) size. Their results supported this hypothesis. Reed et al. (1993) surmised that the results were due to the fact that direct plant-

plant effects are averaged out and that the overall compositional patterns generally reflect the broader, coarser-grained variations in the physical environment. This dominance of micro-scale factors by those operating at a broad scale was evident in research by Crist and Wiens (1994). They examined the factors that influence seed harvest by ants and reported that while individual-level mechanisms involved in foraging may provide information on species interactions or pathways of energy flow in ecosystems, they were less likely to predict harvest rates among colonies than broad-scale factors such as vegetation structure and predator abundance.

These findings were similar to those of Bowers and Dooley (1993), who investigated predation hazard and seed removal by small rodents. Contrary to much of the earlier work on this subject, these authors reported finding seed removal rates to vary more with the macro-habitat features of the habitat patches than those micro-habitat characteristics within each site. Much of the previous work on these taxa focused nearly exclusively on the role of micro-habitat conditions on population variation. Species response to scale are not limited to animals, however. Gibson et al. (1993) examined the interactions of scale and typical management practices employed on grasslands. These authors reported several scale-dependent responses of the vegetation. For instance, they noted that within a soil type (small plot) that mowing effects had a greater effect on the plant community than burning, but

between soil types, burning had a greater affect than mowing.

Scale may have played a role in the present test of the northern bobwhite HSI model. For instance, it is possible that the relationships between habitat suitability and vegetation conditions expressed in the model are based on observations of habitat use by individual coveys, that is, the curves describe factors likely to influence habitat use within the home range rather than the potential for a site to support ≥ 1 covey.

Work by O'Neil (1993) suggested that the scale at which the model was applied in the present study is likely consistent with its intended use. She reported finding a positive correlation ($r = 0.78$, $P < 0.05$) between output from the northern bobwhite HSI model and the density of quail detected on 9 study sites in western Tennessee. Further, conversations with the author of the model suggest that the scale at which the model was tested was appropriate given the data used in the construction of the model.

Models are simplifications of systems for which we wish to gain a better understanding. Identifying those forces that shape habitat selection patterns and incorporating them into a predictive habitat model is challenging. The success of the model is largely determined by our ability to identify those factors that the species is actually responding to or at least those factors that are correlated with those

dimensions of the environment to which the species is responding. The failure of a previously successful model may be an indication that the factors assumed to be responsible for population performance were in fact simply correlates thereof and that there has been an uncoupling of this relationship between the proximate and ultimate factors responsible for habitat occupancy.

Van Horne and Wiens (1991) cautioned against testing a model under conditions different from those under which it was developed. Conditions on nearly all of today's farms have changed dramatically from those days when much of the data upon which the model is based were collected. The failure of the model may be linked to these changes. It may be that the variables in the model were simply correlates of the factors that ultimately determined bobwhite population levels in previous agricultural landscapes. However, not until that farm landscape changed was this evident. In other words, these changes may have precipitated an uncoupling of the relationships between the factors assumed to directly and indirectly determined bobwhite population levels. The success of O'Neil's (1993) test may at least be partly due to the fact that her study sites were not "typical" of today's intensively managed farm lands. Ames Plantation in western Tennessee, the location where her work was conducted, is intensively managed for quail.

Composition Suitability Indices: Was Winter Food Limiting?

The northern bobwhite requires multiple cover types to meet its seasonal habitat needs. Habitats providing high quality winter food, cover, and nest/brood habitat need to be in relatively close proximity of one another. An additional important consideration in managing quail habitat is the proportion of the area providing each of the 3 life requisites in optimum condition. The draft HSI model by Schroeder (1985) suggests that ideal conditions should exist when $\geq 80\%$ of an area provides winter food in optimum condition, 10% of the area is in optimum nest/brood habitat and 20% of the site provides cover in optimum condition. Below 80, 20 and 10%, habitat suitability is assumed to diminish according to the Composition Suitability Indices (Fig. 3).

Winter food had the smallest Composition SI at 116 of the 121 sites. Consequently, it was assumed to be more limiting than either nest/brood habitat or cover. However, as the previous attempts to explain the poor fit of the model suggest, the lack of fit may have little to do with food. Rather, the assumption that 80, 20, and 10% (food, cover, and nest, respectively) represents ideal conditions may be inaccurate. Below I present several lines of evidence that suggest that the absence of a relationship between model output and the performance measure is due to the fact that nest/brood habitat, not winter food, was limiting quail populations

during that period of time the populations were sampled.

Previously it was suggested that pasture/hayland should be considered a source of winter food because the area of this cover type at a station was correlated positively with the difference between observed levels of population performance and levels indicated by the model. Moreover, pasture/hayland had a winter food LRSI of 0.19. However, the analysis of the role of interspersed cover casts some doubt on the role of pasture/hayland as a winter food source. These data suggest that food availability only determined population levels insofar as it replaced nest/brood habitat that was being sought by the species.

The amount of pasture/hayland at a station and OPTNBC were correlated ($r_s = 0.70$, $P = 0.0001$, $n = 121$). Thus, as the amount of pasture/hayland increases, winter food (assuming pasture/hayland is treated as a source of winter food), as well as nest/brood habitat, presumably increase as well. Further, recall that, even after adding pasture/hayland to the estimate of OPTLWF, the mean difference between the number of birds detected and those indicated by the model based on available winter food was still relatively high ($\bar{X} = -0.14$). However, if we assume that nest/brood habitat was limiting and compare population levels with those indicated based on available nest/brood habitat, we find that the mean difference between the number of birds detected and those indicated by the amount of nest/brood habitat

was 0.46 ($n = 48$, $SE = 0.03$). The number of birds recorded at a station never exceed the level indicated by the model, assuming that nest/brood habitat was limiting. Moreover, the performance measure and OPTNBC were correlated positively ($r_s = 0.55$, $n = 121$, $P < 0.0001$, Fig. 24). Thus, the difference between observed levels of quail and those indicated by the model may have little to do with excluding pasture/hayland as a source of winter food, but instead, a result of the possibility that nest/brood habitat, not winter food, was responsible for the number of males detected at station. Nest/brood habitat, more than any single factor considered thus far, provides the best explanation for the absence of a relationship between the performance measure and the amount of winter food at a station, the supposed limiting factor at all but 6 of the 121 stations. The bobwhite's response to available nest/brood habitat is likely responsible for the positive correlation between the performance measure and the amount of pasture/hayland at a station (earlier assumed to be attributable to food resources).

Previously, I suggested that the distribution of crops on the study area may have been at least partly responsible for the observed distribution of quail on the study area. This relationship was discovered while attempting to improve the fit of the model by adjusting the contribution of crop fields to the estimate of OPTLWF. Although the changes did not improve model fit, the effort did provide further

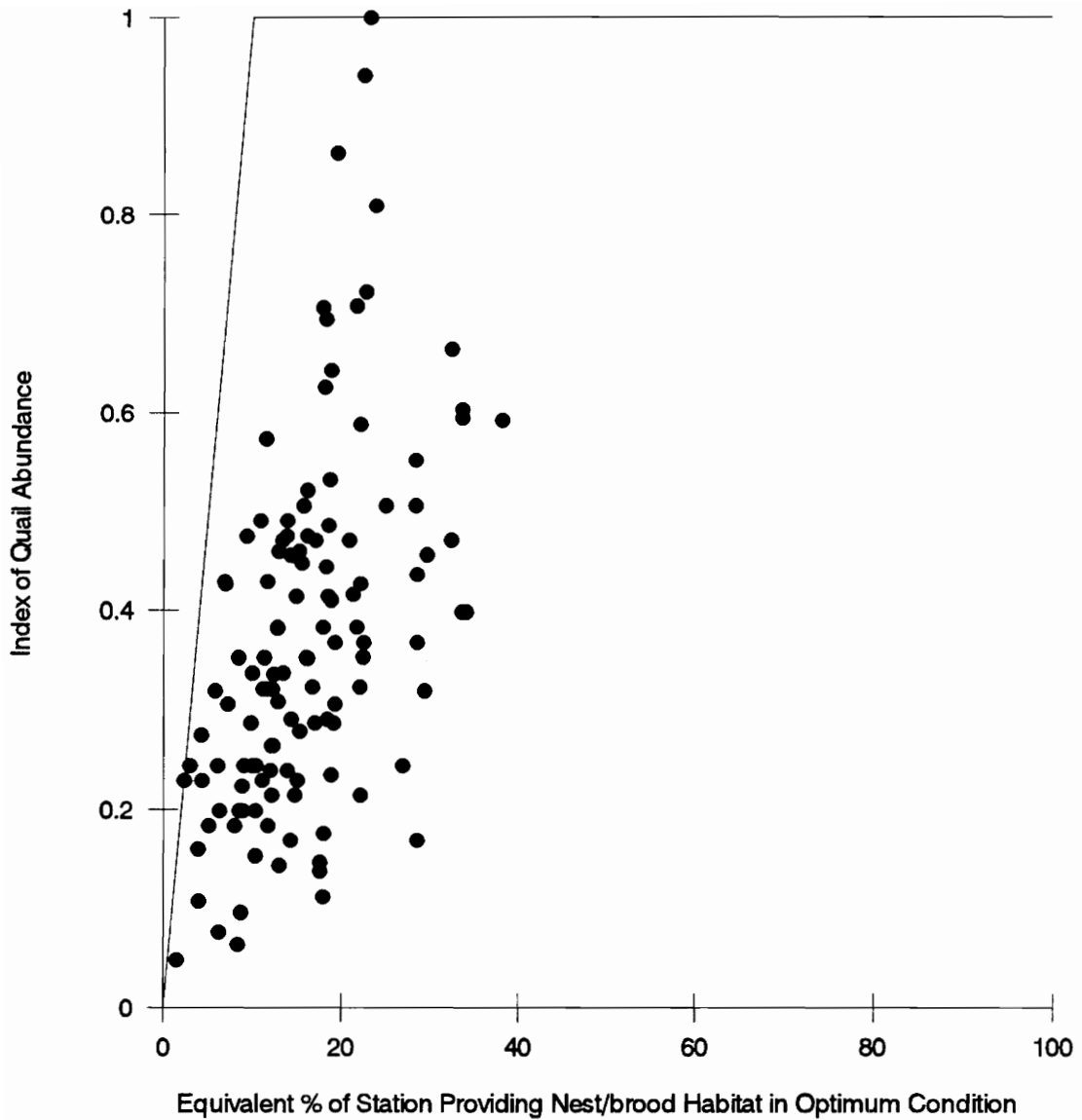


Figure 24. Relationship ($r_s=0.55$, $P < 0.0001$, $n = 121$) between the performance measure and equivalent percent of station providing nest/brood habitat in optimum condition for 121 stations sampled 1986-1991, Halifax County, Virginia.

evidence that a life requisite other than winter food, specifically nest/brood habitat, was limiting quail populations.

I calculated the mean contribution (%) of each of the 28 cover types to the estimate of OPTLWF (Table 13) for both the CRP HSI model and Schroeder's HSI model. Of particular importance are the estimates for crops and high canopy woodlands. Under the CRP HSI model, crops represented on average nearly 19% of the estimate of OPTLWF and high canopy woodlands represented approximately 46%. However, under the HSI model, which reflects overwinter crop management practice and crop type grown, crops represented on average <3% of the estimate of OPTLWF. This reduction is a direct result of incorporating over-winter crop management practice and crop type. Because the sum of "LRSI₂ + SIV3 (Fig. 17)" must be reduced to 1 before adjusting for overwinter crop management practice, which I assumed was "crop harvested, fall plowed," the maximum value for the winter food LRSI in crop fields was 0.1. This is a reduction of just over 800% from the estimate of LRSI under the CRP model. High canopy woodlands however, represented nearly 55% of the estimated available food, more than all other cover types combined. If in fact high canopy woodlands provide little or no nest/brood habitat, as was assumed at the outset (Table 8), then the negative relationship in Figure 19 suggests that nest/brood habitat, rather than winter food, may have been

Table 13. Mean contribution (%) of 28 cover types to estimates of available winter food based on the CRP HSI model for the northern bobwhite and the HSI model developed by Schroeder (1985) and the correlation between estimated available nest/brood habitat and each cover type. Means, standard errors (SE) and correlations (r_s) are based on 121 sites sampled 1986-1991, Halifax County, Virginia.

Habitat	CRP Model		HSI Model		r_s	P
	\bar{X} (%)	SE	\bar{X} (%)	SE		
Woodlands^a						
LOW CANOPY WOODLANDS						
Saplings, light stocking stocking	0.66	0.30	0.76	0.32	-0.04	0.64
Cutover with Saplings, light stocking	0.67	0.39	0.77	0.46	0.02	0.81
Saplings, heavy stocking	0.85	0.21	0.98	0.23	-0.02	0.77
Saplings, heavy stocking; Poles, light stocking	5.5	1.03	6.64	1.24	0.01	0.88
Cutover with Saplings, medium stocking; Poles, light stocking	2.3	0.58	2.6	0.62	-0.17	0.06
Low Canopy Woodlands	10.0	1.26	11.7	1.45	-0.01	0.90
MEDIUM CANOPY WOODLANDS						
Saplings, light stocking; Poles, medium stocking	0.55	0.08	0.68	0.10	-0.08	0.39
Poles, medium stocking	0.19	0.06	0.22	0.07	0.17	0.07
Saplings and Poles, medium stocking	0.60	0.10	0.79	0.14	-0.21	0.02
Medium Canopy Woodlands	1.33	0.14	1.68	0.18	-0.21	0.02
HIGH CANOPY WOODLANDS						
Saplings, Pole and Mature, light stocking	20.6	1.82	23.8	2.02	-0.41	0.001
Pole and Mature, light stocking	2.3	0.63	2.5	0.65	0.29	0.002

Table 13. Continued.

Habitat	Winter Food					
	CRP Model			HSI Model		
	$\bar{X}(\%)$	SE	$\bar{X}(\%)$	SE	r_s	P
Saplings and Pole, medium stocking; Mature light stocking	22.2	1.84	26.0	2.02	-0.38	0.001
Saplings, heavy stocking; Pole and Mature, light stocking	1.8	0.54	2.12	0.58	-0.10	0.28
High Canopy Woodlands	46.9	2.08	54.5	2.02	-0.81	0.001
Grazed Woodlands						
Saplings, Pole and Mature, light stocking	1.0	0.47	1.19	0.57	0.22	0.02
Pole and Mature, light stocking	0.28	0.13	0.34	0.16	0.25	0.005
Saplings and Poles, medium stocking; Mature, light stocking	0.48	0.25	0.56	0.28	0.11	0.22
Saplings, heavy stocking; Pole and Mature, light stocking	0.21	0.15	0.22	0.15	0.17	0.07
Saplings, light stocking	0.27	0.13	0.29	0.13	0.11	0.23
Cutover with Saplings, light stocking	0.09	0.09	0.16	0.16	0.14	0.14
Saplings, light stocking; Poles medium stocking	0.14	0.08	0.15	0.08	0.04	0.62
Cutover with Saplings, medium stocking; Poles, light stocking	0.05	0.58	0.05	0.62	-0.03	0.78
Cutover with Saplings, medium stocking; Poles and Mature, light stocking	0.03	0.03	0.03	0.04	-0.09	0.33
Saplings, heavy stocking	0.01	0.00	0.01	0.004	-0.06	0.49
Poles, medium stocking	0.16	0.15	0.17	0.17	0.01	0.88
Saplings and Poles, medium stocking	0.02	0.02	0.02	0.02	0.09	0.30

Table 13. Continued.

Habitat	Winter Food				r _s	P
	CRP Model	SE	X̄(%)	SE		
Other Habitats						
Crop	18.7	1.5	2.8	0.34	0.24	0.01
Pasture/hayland	0.0	-	0.0	-	0.69	0.001
Fallow field	17.8	1.04	23.1	1.43	0.14	0.13
Fallow with saplings	2.6	0.36	3.0	0.40	-0.07	0.42

^aWoodlands were classified according to composition (saplings < 3cm dbh; 3 ≤ poles < 25 cm dbh; mature > 25 cm dbh) and relative stocking rates (light < 25%; 25 ≤ medium < 50; and heavy > 50 % coverage) in each size class. Stocking rates are an "ocular" estimate of % coverage.

limiting during the time the populations were sampled. The percent of the station in high canopy woodlands and the percent of the station providing nest/brood habitat in optimum condition were correlated negatively ($r_s = -0.81$, $P < 0.001$, Table 13). If quail were in fact limited by nest/brood habitat, and high canopy woodlands were not a source of such habitats, then increases in winter food, and hence high canopy woodlands, would lead to a decrease in the number of calling males; Figure 19 supports this proposition. From these analyses, it is unclear as to whether the HSI or the CRP HSI model is a better measure of the true value of crop fields as a winter food source. However, the data do suggest that nest/brood habitat, not winter food, was largely responsible for the observed distribution of quail at the time of sampling.

In the HSI model for the northern bobwhite, maximum population performance is expected to occur when OPTNBC is $\geq 10\%$, assuming both food and cover resources are at or above 80 and 20%, respectively (Fig. 3). At levels $< 10\%$, population performance will be proportional to the amount of nest/brood habitat resources available. If in reality, however, optimal conditions were not realized until the equivalent percent of the area providing optimal nest/brood habitat equaled or exceeded some level $\geq 10\%$, the observed performance of the population would logically fall short of the expected performance (Fig. 25). This suggests that

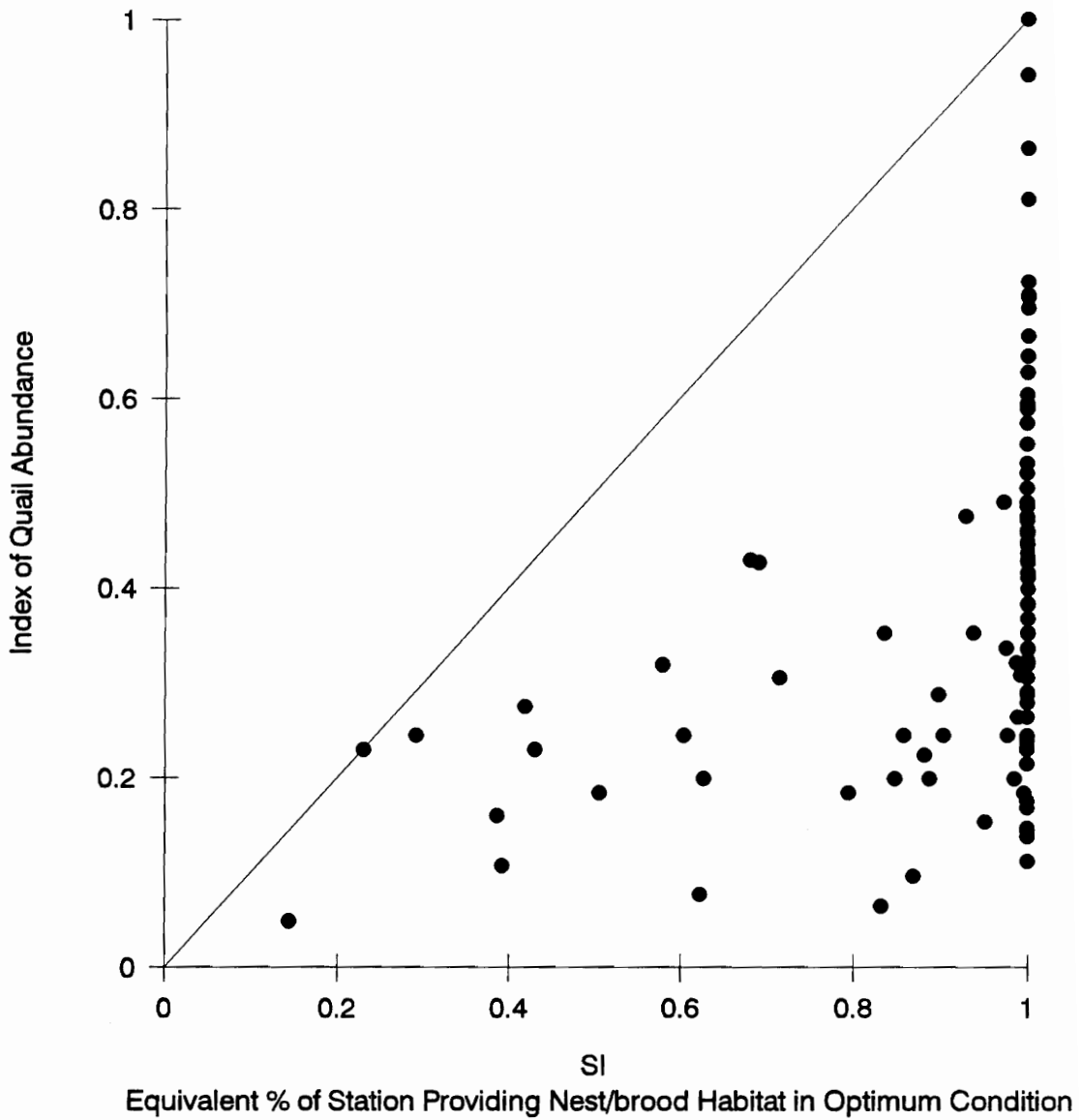


Figure 25. Comparison of observed population performance with levels indicated by the nest/brood habitat component of the CRP HSI model. The 45° represents a habitat-imposed upper limit to population performance. Sites (n=121) were sampled 1986-1991, Halifax County, Virginia.

maximum population performance may not occur until OPTNBC exceeds the 10% threshold level. Quail appeared to respond to increases in nest/brood habitat for most of the range sampled (Fig. 24, $r_s = 0.55$ $P < 0.001$, $n = 121$). There is however, ≥ 1 alternative explanation for the distribution of points below the 45° line in Figure 25.

The model being evaluated was developed for the species' entire range. Population performance across the species' range may range from 2.72 males calling per stop to > 10 males per stop (Table 3). To accommodate such a range of variation, model developers typically use either an average value for the performance measure observed at a given level of the independent habitat parameter/life requisite or the maximum ever observed at that level of the variable in model construction. In the case of the latter, the 45° degree line in Figure 25 would represent an upper limit to population performance at each level of the parameter being evaluated. In either case (that is, the use of maximum values or averages in the construction of the model), however, the fit of the draft model is consistent, given the data in Table 3. Local quail populations were well below the highest values recorded for the states surveyed and probably below average for the species' range. That being the case, the position of the points below the line is not unreasonable. However, I believe the concentration of points below the line in

Figure 25 is due primarily to the fact that maximum quail densities will not be realized until OPTNBC is above the proposed 10% threshold. An SI curve developed for this variable using the present data supports this hypothesis.

Means, rather than maximum values, for the performance measure at each level of the independent parameter were used. However, because no 2 stations had identical values for OPTNBC, the data were categorized at 3% intervals from 0 to 40%, which was the maximum, and the mean number of birds detected per visit estimated for each of the categories.

Based on the data in Figure 26, maximum population performance on the study area is not likely to occur until approximately 77% of the station is in optimum nest/brood habitat. Changing the threshold value from 10 to 80% for OPTNBC increased the correlation (r_s) between model output and the performance measure from 0.09 ($P = 0.35$) to 0.40 ($P = 0.001$). The amount of nest/brood habitat was able to account for nearly 80% ($r^2 = 0.79$, $P < 0.001$, $n = 13$) of the variation in quail numbers when means rather than the original 121 values were considered.

The HSI model for the northern bobwhite states that cover may be limiting when the equivalent percent of an area providing this life requisite in optimum condition is $< 20\%$. Because I found no relationship ($r_s = 0.09$, $P = 0.35$, $n =$

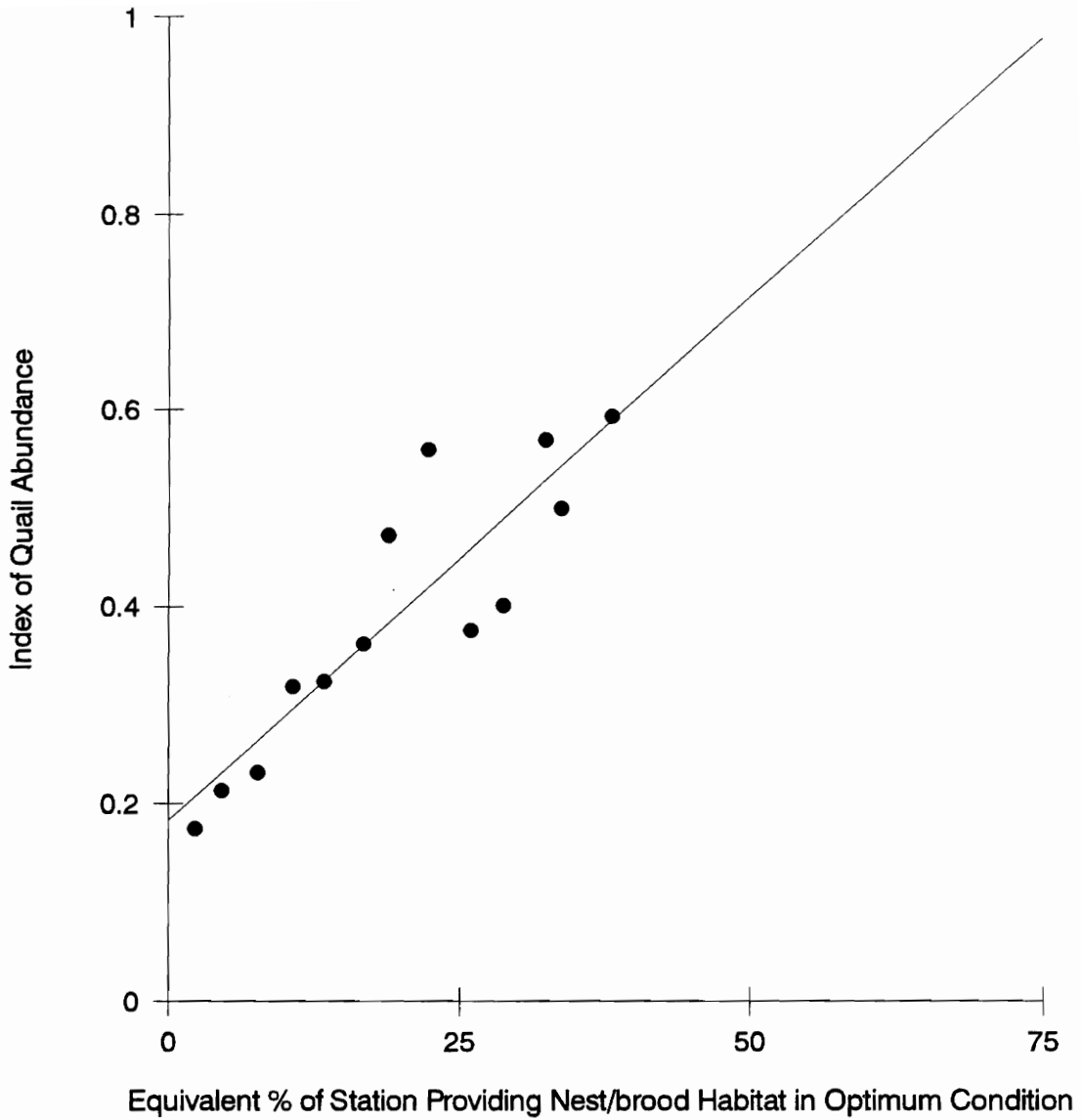


Figure 26. Proposed suitability index curve for equivalent percent of area providing nest/brood habitat in optimum condition. Observations reflect average population performance based on 121 original observations collected 1986-1991, Halifax County, Virginia. Nest/brood habitat accounted for 81% ($P < 0.001$) of the variation in the performance measure.

121) between available winter food and the performance measure, some level > 20% may be a more appropriate threshold value for cover. That is, winter food may have been erroneously identified as the limiting factor when in fact cover was. It is apparent that this was not the case (Fig. 27). In fact, population performance appeared to be limited when OPTCOV exceeded approximately 10%. It appears that cover has the potential to limit populations, but only indirectly, possibly by displacing resources that were directly limiting quail numbers at the time of sampling.

The model identified nest/brood habitat as the limiting life requisite at only 3 of the 121 sites sampled. However, as previous analyses have suggested, I believe nest/brood habitat may have been limiting at most, if not at all 121 stations. Although the HSI model (Schroeder 1985) suggests that nest/brood habitat has the potential to limit populations when the equivalent percent of area providing optimal conditions falls below 10%, it appears that quail numbers on my study area are likely to be nest limited to levels as high as 80% OPTNBC or more. This may account for the negative relationship between the performance measure and OPTCOV and the absence of a relationship between winter food and the performance measure.

Habitats providing cover and nest/brood habitat generally were negatively

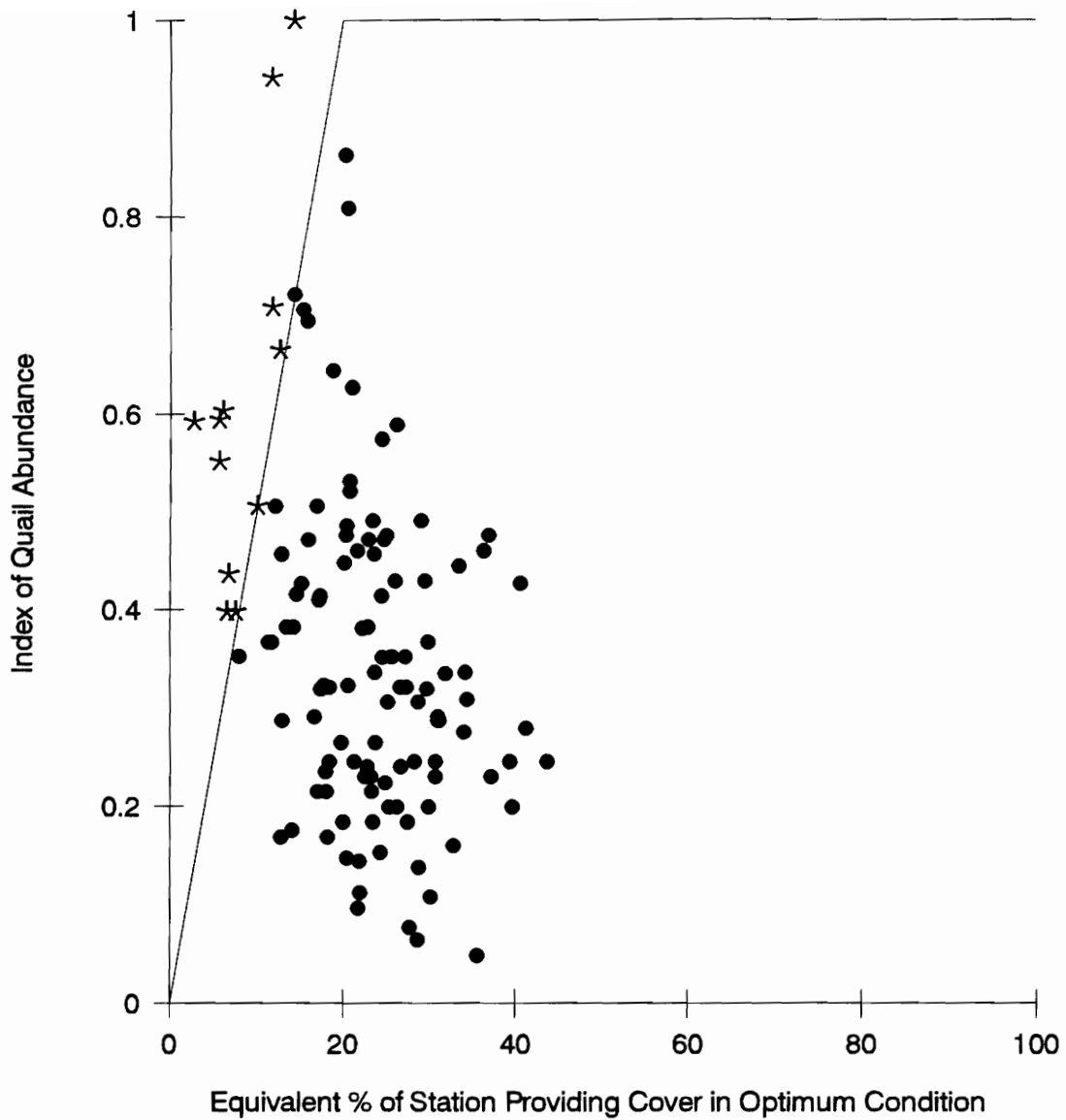


Figure 27. Relationship ($r_s = -0.41$, $P < 0.001$, $n = 21$) between the performance measure and equivalent percent of station providing cover in optimum condition. Asterisks indicate those sites where population performance exceeded levels indicated by the model. Stations were sampled 1986-1991, Halifax County, Virginia.

correlated with one another (Fig. 28). Ungrazed high canopy woodlands were the single largest source of cover on average, for the 121 sites sampled (Fig. 29). Because this habitat type did not contribute to the estimate of available nest habitat (Table 8), any increase in these cover types resulted in a decrease in nest/habitat (Fig. 30). Consequently, as mature timber replaced open land (pastures and cropland), protective cover replaced nesting habitat. If nesting habitat was indeed the limiting life requisite at the time of sampling, this would explain the relationship between the performance measure and OPTCOV (Fig. 27).

Spring Call Counts: A Reliable Measure of Population Performance?

The use of spring whistle counts in studies of northern bobwhite has generated a great deal of debate among researchers and managers over the past 45 years. Whether or not spring call counts can be used as an index of fall population levels has been contested. Stauffer (1993), who provided a thorough review of the opinions on this index, concluded that " call counts can be used to track trends in population levels over time and to compare relative densities in different areas." Despite such optimism, I think Stoddard (Carmichael, pers. commun.) may have more appropriately estimated

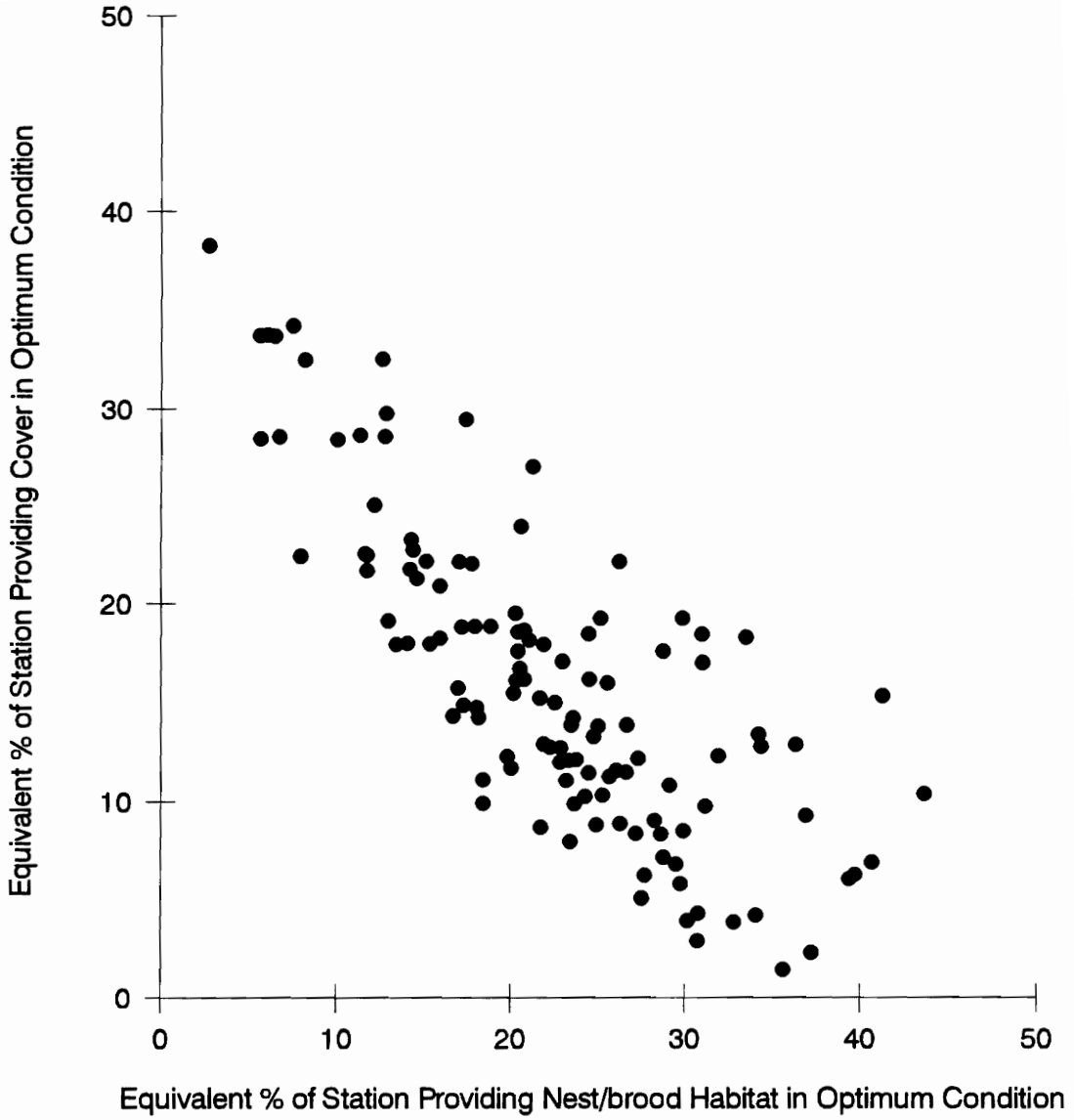


Figure 28. Relationship ($r_s = -0.77$, $P < 0.001$) between equivalent percent of area providing nest/brood habitat and cover in optimum condition. Data were collected at 121 sites sampled 1986-1991, Halifax County, Virginia.

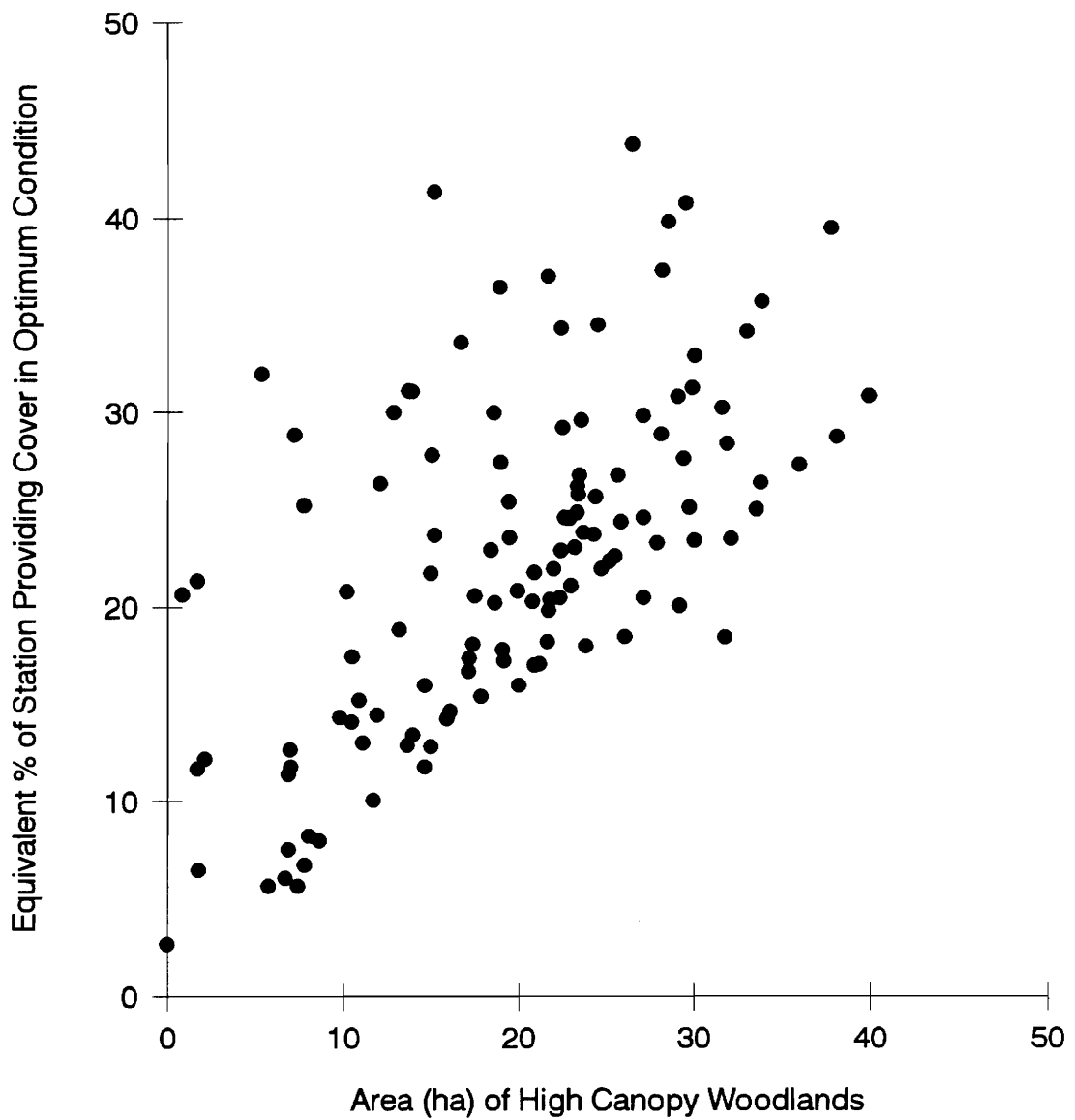


Figure 29. Relationship ($r_s = 0.61$, $P < 0.001$, $n = 121$) between area (ha) of high canopy woodlands and equivalent percent of station providing cover in optimum condition. Data are from 121 sites sampled 1986-1991, Halifax County, Virginia.

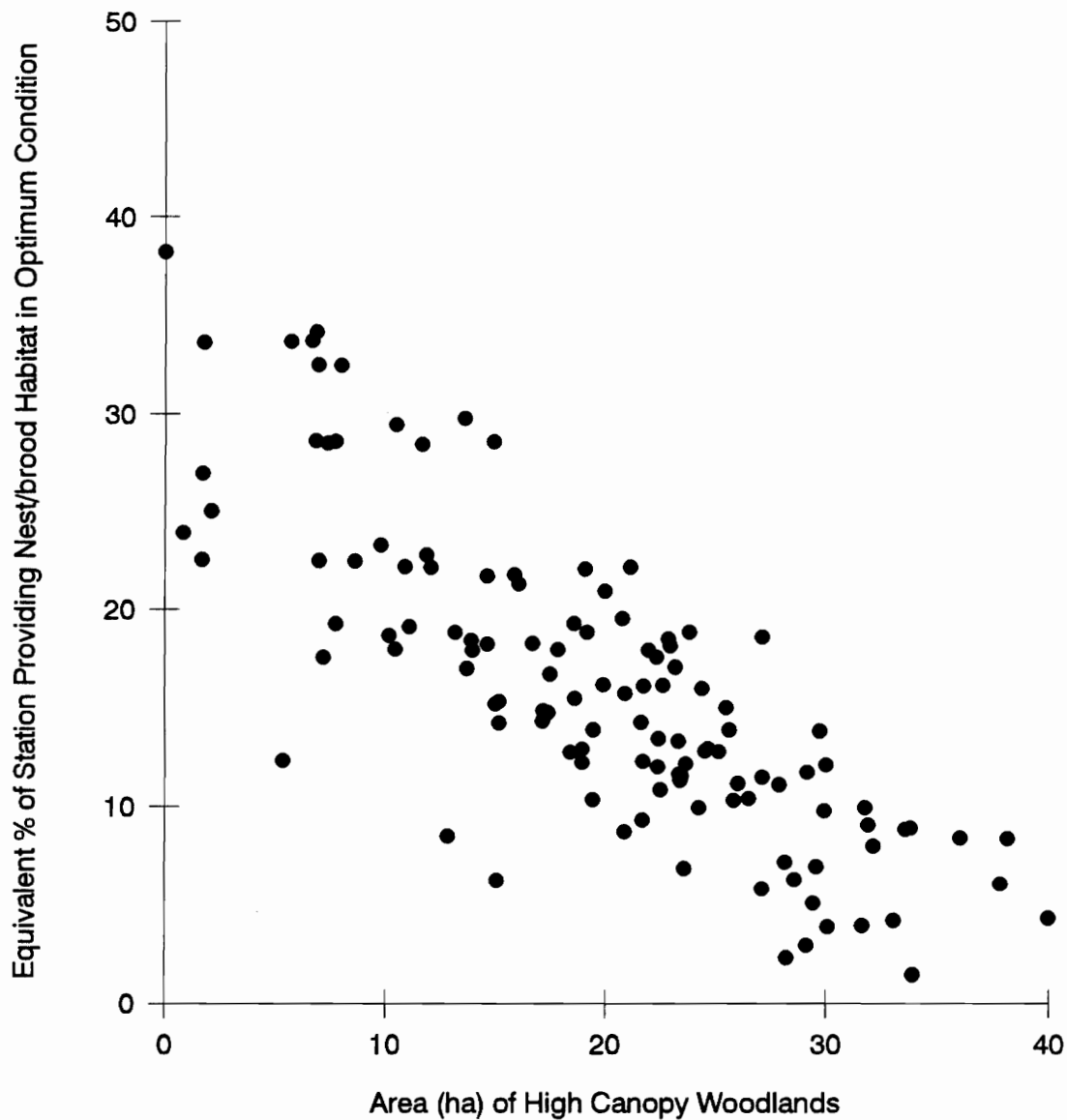


Figure 30. Relationship ($r_s = -0.81$, $P < 0.001$, $n = 121$) between area (ha) of high canopy woodlands and equivalent percent of station providing nest/brood habitat in optimum condition. Data are from 121 sites sampled 1986-1991, Halifax County, Virginia.

their worth with his response to "what does that whistle mean?", to which he quipped, "that a male is over there." Many states have abandoned their use of call counts in favor of late-summer roadside brood counts as an index of fall levels.

Despite its limited nature, there is some inductive evidence to suggest that there may not be a direct relationship between call count data and population density. Using 8 years of density data obtained in December and call count data during July, Dimmick (unpubl. data) failed to detect any correlation between the 2 measures. He reported that the lowest December population (908 bobwhites) and the highest (2210) were preceded by nearly identical call counts of 38.0 and 37.8 whistles per station, respectively. Backs et al. (1981) also found no relationship between the number of whistling males and any of the 6 density indices generated on 24 farms in southeastern Indiana. Back's was able to account for 61% of the variation in the maximum number of birds observed per ha using various measures of interspersed and land use characteristics. However, he reported finding no relationship between the number of males detected on these 24 farms during spring visits and any measure of density including total birds observed, total coveys observed, and mean covey size.

Other research suggests that indices based on vocalizations may at best provide a very crude estimate of abundance. Researchers in Missouri concluded a 7-

year investigation of the relationship between mourning dove call counts and associated nesting activity by stating that, "Call count data may help detect gross differences in numbers of dove nests and breeding doves from year to year and habitat to habitat. However, it is unlikely that such data are adequate for precise predictions of nesting effort or production of young..." (Armbruster and Baskett 1985:23). Their conclusions, however, are based on only 2, 61 ha study plots, where years were used as replicates. They found the number of calling males was not correlated ($r=0.06$, $P > 0.10$) with nests on 1 area, yet highly correlated on the other ($r = 0.86$, $P < 0.03$). Thus, vocalizations may not reflect true underlying population levels.

DeMaso et al. (1992) cautioned against using northern bobwhite covey calls as anything but a crude measure of relative abundance. Line transect methodology was used to estimate the density (#/ha) of quail on 6 sites in southern Texas. Corresponding morning covey call counts were conducted with the intent of testing the hypothesis of no relationship between the 2 measures. The number of coveys heard was regressed on their estimate of density, an index of vegetation biomass, and wind velocity. The model was able to account for 47% of the variation in the number of coveys heard. The use of call count data in the present investigation, which was assumed to provide an index of abundance, may have contributed to

model failure because the number of calling males may simply be an index of the number of calling males and not the overall population.

The ideal measure of population health and habitat quality would be the number of individuals surviving to reproduce. Logically, the most valuable estimate is also the most costly to secure. As a result, wildlife managers and biologists rely quite heavily on relatively easy to obtain measures of abundance, despite warnings from Van Horne (1983). In a few instances, complete censuses are possible. However, most often we must settle for indices of population size and health. With hunted species such as the northern bobwhite, we have typically focused our interest on population size immediately prior to hunting season, for obvious reasons. Knowledge of fall population levels is important. However, I question whether indices of fall population levels should be used as a benchmark against which other measures of relative population size should be compared, specifically spring call counts.

The use of spring call counts has been discouraged because, as pointed out, they are generally poor predictors of fall population levels (but see Curtis et al. 1989). Much of this skepticism is derived from comparisons of harvest data with spring call counts. Stauffer (1993) however, questioned the scientific rigor of harvest data and cautioned against their use. Moreover, the fact that limited research

has failed to demonstrate a relationship between fall densities and spring whistle counts does not seem reason enough to completely discount such counts. As Dimmick (pers. commun.) pointed out, the fact that he failed to find a relationship between spring and fall population estimates may be due to population levels. He proposed that population levels on his study area may have exceeded some upper limit where the relationship begins to fall apart. Further, he used only 2 years of data from an area in western Tennessee that is intensively-managed for quail. Lastly, I question the reliability of spring whistle counts at relatively high population levels.

CONCLUSION

Spring call count data were used in the present investigation to test the CRP HSI model, a hypothesis proposed to account for variability to in northern bobwhite population performance. The original model failed. Multiple factors may have contributed to the results. Ultimately however, it failed for one of 2 reasons; either the performance measure was not a measure of potential population performance, as it was assumed to be, or the model was wrong. In my opinion it was the latter. The performance measure is based on 6 years of data. Those sites that had relatively more quail, consistently had more quail. Moreover, those same sites had consistently

more nest/brood habitat. In conclusion, I suggest that the results of this study justify a modification of the northern bobwhite HSI model, at least for Halifax county and the Piedmont physiographic region of Virginia and North Carolina. Nest/brood habitat, not winter food, as the model predicted, appears to be limiting the quail population on my study area. The model should be adjusted to reflect this.

CHAPTER 2: EVALUATING THE POTENTIAL IMPACT OF THE CRP ON NORTHERN BOBWHITE

INTRODUCTION

Agricultural policy has had, and will continue to have a significant impact on both terrestrial and aquatic wildlife. From 1936 to 1942, nearly 12% of the nation's farmland was idled as a result of the 1936 Farm Act (Harmon 1987). As a result, an already expanding pheasant population grew even larger. Similarly, following sharp population declines associated with increased agricultural production during WWII, pheasant populations experienced tremendous growth following the 1956 Soil Bank Program. In the mid-1950s, South Dakota's pre-harvest pheasant population was estimated at between 4 and 6 million birds. Following the retirement of 728,460 ha of cropland throughout the state, the pheasant population was estimated at between 8 and 11 million birds (Harmon 1987). These gains however, were short-lived.

Economic conditions throughout the world led to the "plow-out" of the 1970s (Bedenbaugh 1987). Although some producers realized short-term profits from this "ditch to ditch" farming, the long-term net effect was exacerbation of an already-present overproduction problem. It was precisely for this reason, i.e.,

overproduction, and not the need to conserve soil and ensure water quality, that farm program benefits to wildlife were often limited and short-term in nature. For natural resource benefits to be realized, an agricultural policy with soil conservation and water quality receiving at least equal concern as overproduction is necessary. The Conservation Reserve Program (CRP) of the 1985 federal Food Security Act may be part of a long-term solution to at least partially restore wildlife resources previously lost.

The Conservation Title of the 1985 federal Food Security Act made it possible for farmers to simultaneously reduce soil erosion and related off-site damage, improve water quality, and earn money by enrolling their highly-erodible cropland in the CRP. This is the largest of all land retirement programs for conservation purposes in U.S. history (Ervin 1989). To date, 14.8 million ha have been enrolled (Osborn 1993). In exchange for annual rental payments farmers must agree to 1) implement the conservation plan of operation provided by the Agricultural Stabilization and Conservation Service (ASCS), 2) place the acreage in the CRP for ≥ 10 years, 3) not use the land for agricultural purposes unless permitted, 4) establish permanent vegetative cover (trees, native grasses and legumes, introduced grasses and legumes, wildlife habitat or field windbreaks), 5) not conduct harvesting or grazing or make commercial use of forage, and 6) not

plant trees, unless permitted (Woods and Sanders 1987). Approximately 32,376 ha are enrolled in Virginia. Nearly 50% of the enrolled land has been planted to introduced grasses and legumes (Conservation Practice 1) with an additional 37% being planted to loblolly pines (Conservation Practice 3, A. Allen, Mid-continent Ecological Service Center, unpublished data).

Experts believe that if the 18.2 million ha national goal is reached, there could be an estimated 10 billion dollars in natural resource benefits, primarily from improved surface water conditions and wildlife habitat (Ribaudo et al. 1989). If this enrollment goal is reached, the total amount of land to be retired under the CRP will still represent only a modest 15% of all U.S. farmland. Even so, Jahn (1988) believed that the potential of the CRP to improve wildlife habitat is comparable to that of the Soil Bank Program of 1956.

Studies have repeatedly shown that pheasants and other grassland birds have increased significantly in response to the undisturbed cover provided by the Soil Bank (Jahn 1988). Berthelsen et al. (1989) expected positive responses from pheasant populations in the Southern High Plains of Texas as a result of the CRP. Dunn et al. (1993) stressed that there is likely to be a multitude of ecological benefits from the program if administrators encourage more tree planting. Johnson and Schwartz (1993a and 1993b) proposed that the decline of several species of

prairie birds was due to the conversion of perennial grassland habitat to annually-tilled cropland. They found several of these affected species to be abundant in CRP fields. The authors noted that CRP fields provided suitable breeding habitats for these species. Their efforts revealed the tremendous value of restored grasslands for nongame bird species. In many areas, it appears that waterfowl are likely to benefit as well (Kantrud 1993). Recent research suggested that CRP fields in Minnesota and North Dakota are likely to provide more secure nesting cover for upland nesting ducks than Waterfowl Production Areas (WPAs) in these states. Kantrud attributed this increase in nest success rate to 2 factors - distance from a water source, and the size of the CRP fields relative to the WPAs. Efforts in south-central South Dakota by Gould and Jenkins (1993) revealed that the CRP enhanced habitat options for white-tailed deer management. Whitworth and Martin (1990) reported significant benefits to benthic macroinvertebrates and fish communities in aquatic ecosystems in first and second-order streams draining agricultural fields as a result of installing vegetative filter strips paralleling streams, lakes, and estuaries. The land-use conversions taking place under the CRP may result in the enhancement of habitats of many farmland wildlife species, both game and nongame (Isaacs and Howell 1988).

Although pheasant populations and many species of waterfowl and grassland

birds have responded favorably to the CRP, the response of the northern bobwhite is likely to be much more variable. Although CRP fields are likely to have inherent value (Burger et al. 1990), it is unlikely that the actual value of the CRP will be a linear function of the total area enrolled. Because the bobwhite is sedentary, moving little within an average home range of 5-40 ha, the primary determinant of habitat quality is the proximity of daily and seasonal habitat needs (Dimmick 1992). High quality habitat consists of a mixture of woody and herbaceous cover. Consequently, field size, placement, and proximity to other habitats meeting the species' needs, rather than absolute quantity, will determine, to a large extent, the northern bobwhite's response to the CRP (Burger et al. 1990, Stauffer et al. 1990, Roseberry et al. 1994). More specifically, the impact of the CRP on northern bobwhite populations will be determined by 1) the amount of CRP land present, 2) the suitability of this land for bobwhite use, 3) the suitability of replaced and remaining cropland for bobwhite use, 4) the juxtaposition of CRP fields with other habitat components, and 5) the composition and quality of existing bobwhite habitat, most especially, which life requisites are limiting (Roseberry and David 1994). The program's impact will be determined as much by the structural characteristics of the CRP fields as by the placement of these fields in the agricultural landscape. Contrary to the opinion of these earlier researchers, there is some evidence to

suggest that an evaluation of the impact of the CRP on northern bobwhite populations of the Piedmont physiographic region of Virginia will be much more direct.

Stauffer et al. (1990) predicted that the CRP is likely to increase the availability of suitable nesting and brood rearing habitat in those areas of the Commonwealth affected by the CRP. Similarly, Fies (1992) proposed that a loss of habitat due to changing land use in general, and suitable nest/brood habitat in particular, are responsible for the present status of much of Virginia's quail population. Moreover, a test of the HSI model for the northern bobwhite (Chapter 1) strongly suggests that nest/brood habitat is limiting quail populations in Halifax County, Virginia, and possibly other areas throughout the Piedmont physiographic region of Virginia and North Carolina. Finally, my data (Chapter 1) suggest that, unless lands enrolled in the CRP are concentrated, which they do not appear to be (Pierce, pers. commun.), thus reducing landscape diversity, the interspersions of cover types on my study area is adequate and not likely to be threatened by the CRP. Consequently, placement of these fields is not likely to be as important as the actual micro-habitat conditions these fields provide relative to the conditions they are replacing. Thus, the objectives of this study were 1) describe micro-habitat conditions in crop fields pre and post-enrollment in the Conservation Reserve

Program and 2) evaluate these changes in light of their impact on the life requisite that appears to be limiting quail populations on the study area - nest/brood habitat.

METHODS

As of July 1991, approximately 33,000 ha of Virginia farmland had been enrolled in the CRP (Allen, unpubl. data). Of the 13 Conservation Practices (CP) available to landowners, CP1 (introduced grasses, primarily fescue) and CP3 (trees, typically loblolly) constituted nearly 83% of the enrolled land. Consequently, this investigation focused on conditions associated with these 2 CPs.

Because conditions in CRP fields will undoubtedly change over time, most notably those sites planted to pines, I selected CP3 sites according to their age of establishment. Canopy closure and subsequent changes in the herbaceous and woody vegetation layers, factors most directly affecting suitability of quail habitat, generally occurs at about 8 years-of-age for loblolly pine. Therefore, all potential sites were classified as either $<$ or \geq 8 years-old. Although at the time of sampling, the CRP was just 6 years old, I was able, with the assistance of 2 state foresters, to locate older ($>$ 8 years) sites. Although not technically CRP fields, these sites could be treated as such because they were crop fields prior to being planted to loblolly pines. In addition, I examined conditions in a series of loblolly pine plantations

(CP3) that had received some level of commercial thinning. Finally, I documented conditions in a representative sample of crop fields to serve as reference conditions.

Halifax County Agricultural Stabilization and Conservation Service (ASCS) and Soil Conservation Service (SCS) personnel were contacted for information regarding CRP enrollment. All farms enrolled through the 9th sign-up were considered. Twenty-five sites per CP were identified from ASCS and SCS records and located on aerial photos. Photocopies of the photos were used in locating individual fields on each farm. A single 50 m transect was used to estimate vegetation conditions in each field (mean field size for Halifax County is 1.8 ha). The starting point for the transect was randomly selected, as was the direction of travel. Point sampling (Hays et al. 1981) was used to generate estimates for % canopy cover of herbaceous vegetation, % of herbaceous canopy that is grass, and % bare or lightly littered ground. These 3 variables compose the nest/brood habitat life requisite of the CRP HSI model for the northern bobwhite (Chapter 1). Data for the CRP fields were collected July 10th through August 12th, 1991. Vegetation data in crop fields were collected late August, 1991.

RESULTS

Nest/brood habitat vegetation data were collected on a total of 46 farms

distributed throughout Halifax County. I sampled a total of 97 sites. The number of fields sampled per practice ranged from 14 for CP1 fields to 26 for CP3 fields with commercial thinning (Table 14). Conditions in each of the 5 field types varied considerably. Crop fields and CP3 fields > 8 years-old had more ($P < 0.01$) bare ground than the 3 other field types. CP1 fields provided the least amount of bare ground at just under 19%. All field types except those planted to pines < 8 years-old had more ($P < 0.01$) available ground than CP1 fields.

Suitability Index (SI) values for bare ground (GRNDNS) ranged from 0.38 for CP1 fields to 0.7 for thinned CP3 stands. Because of sample size differences, statistically significant differences among the field types were inconsistent. While there was no difference between the 2 extreme values for the SI for bare ground, the SI value for thinned CP3 stands (0.70) was $> (P < 0.01)$ that for CP3 sites > 8 years-old (0.51), as well as crops (0.44, Table 14).

Those sites with the greatest amount of bare ground had the least amount of herbaceous vegetation; crop fields were an exception. Crop fields had relatively high (64%) coverage of herbaceous cover, given that they also had consistently high amounts of bare ground. CP3 fields < 8 years-old and CP1 fields ranked 4th and 5th, respectively, in terms of bare ground. The converse was true for canopy cover

Table 14. Mean nest/brood habitat Life Requisite Suitability Index (NBLRSI), means (%), standard errors, and mean SIs for % bare or lightly-littered ground (GRNDNS), % herbaceous canopy cover (VCVHE01), and % of herbaceous canopy that is grass (VRCGR01) for crop fields, Conservation Reserve Program (CRP) Conservation Practice 3 (CP3) fields < 8 years-old, CP3 > 8 years-old, CP3 thinned, and CP1 fields < 8 years-old sampled July-August, 1991, Halifax County, Virginia. Variables are from the CRP HSI model for the northern bobwhite (Chapter 1).

Field Type (n)	% Bare or lightly-littered ground			% Herbaceous canopy cover			% of herbaceous canopy that is grass			NBLRSI
	\bar{x} (%)	SE	SI	\bar{x} (%)	SE	SI	\bar{x} (%)	SE	SI	
Crop (20)	81.5a	4.9	0.44a ^a	63.9a	7.4	0.57a	81.1a	6.7	0.64a	0.33a
CP1 (14)	18.9b	5.7	0.38ac	90.4c	4.0	0.54a	73.6a	6.3	0.81b	0.34a
CP3 < 8 yrs (16)	32.6b	6.9	0.54ab	82.6ac	3.8	0.65a	74.1a	4.4	0.83b	0.50a
CP3 thinned (26)	63.9c	4.9	0.70bc	3.8b	1.1	0.02b	27.7b	8.0	0.33c	0.04b
CP3 > 8 yrs (19)	82.4a	3.6	0.51a	6.6b	3.7	0.05b	32.5b	9.8	0.37c	0.05b

^aMeans within a column followed by the same letter are not different ($P < 0.01$). Pairwise comparisons were performed using Multiple Response Permutations Procedures running on Blossom Statistical Software (1992). Tests were run after rejecting

$$H_0: \mu_{\text{crop}} = \mu_{\text{CP1}} = \mu_{\text{CP3 < 8 yr}} = \mu_{\text{CP3 thinned}} = \mu_{\text{CP3 > 8 yr}}$$

of herbaceous vegetation. Estimated canopy cover of herbaceous vegetation was 90.4% in CP1 fields and 82.6% in CP3 sites < 8 years-old (Table 14). Herbaceous canopy cover in thinned CP3 fields and those > 8 years-of-age was predictably low, given estimates of bare ground. Thinned stands had slightly < 4% and those > 8 years-old had only 6.6% herbaceous canopy cover. Suitability Index values for herbaceous vegetation ranged from 0.02 for thinned CP3 stands to 0.65 for CP3 sites < 8 years-old. Thinned stands and those > 8 years-old provided less ($P < 0.01$) herbaceous cover than the other 3 stand types, which did not differ from each other (Table 14).

Grass represented a relatively large component of the herbaceous canopy in crop fields, CP1, and thinned CP3 sites, averaging slightly > 76% of the herbaceous cover. These 3 field types had more ($P < 0.01$) relative proportion of grass than both thinned CP3 stands and those > 8 years-old. Grasses represented approximately 30% of the herbaceous canopy in the latter 2 stand types. Suitability Index values for percent of herbaceous canopy composed of grass ranged from 0.33 for thinned CP3 stands to 0.83 for CP3 stands < 8 years-old. The difference between these 2 was significant ($P < 0.01$). CP1 fields, typically dominated by fescue and other non-native cool season grasses, had a slightly lower (0.81) SI for grass cover than CP3 sites < 8 years-old. The SI for this variable in thinned CP3

sites and those > 8 years-old was predictably low at 0.33 and 0.37, respectively (Table 14).

Because of extremely low SIs for herbaceous cover, estimates for NBLRSI were essentially 0 for thinned CP3 sites and those > 8 years-old. Estimates for these 2 field types were < ($P < 0.01$) all other field types, which did not differ ($P < 0.01$) from each other. Crop fields and CP1 sites were nearly identical at 0.33 and 0.34, respectively (Table 14). CP3 sites < 8 years-old averaged slightly higher at 0.50.

DISCUSSION

Results from Chapter 1 strongly suggested that nest/brood habitat is far and away the most limiting of all 3 life requisites. The findings from the present chapter suggest that the impact of the CRP on the nest/brood habitat life requisite, and ultimately quail populations, is likely to be positive, at least initially. The long-term effect is somewhat less certain.

Although the differences were not significant ($P < 0.01$) the data suggest that the conversion of active crop fields to CP1 sites is likely to have a slight positive net effect on conditions that influence the quality and quantity of nest/brood habitat. I would speculate that the actual benefit realized is going to be > the data in

Table 14 suggest. Nest/brood habitat measurements were made in crop fields in late August. I elected to sample at this time so as to get a reasonably accurate estimate of what we might expect crop fields to provide in terms of winter food. Had I sampled during late-spring/early-summer, the peak of the nesting and brood rearing seasons, I feel certain that the estimates for bare ground and herbaceous vegetation would have been higher and lower, respectively, and ultimately NBLRSI would have been lower. Thus, the estimate for NBLRSI for crop fields is likely an overestimate of actual conditions found in this habitat type during the nesting and brood rearing months. Consequently, a conservative estimate of the effect of converting crop fields to CP1 sites might be no net gain. However, based on personal observation, I would predict a slight to moderate positive impact. Stauffer et al. (1990) also predicted that the addition of CP1 fields to the agricultural landscape would benefit quail, primarily through the addition of nesting and brood rearing habitat.

Crop fields planted to pines should provide more suitable conditions for nesting and brood rearing than the conditions replaced. Again, although no significant ($P < 0.01$) difference was detected between crop fields and CP3 sites < 8 years-old, I propose that real differences are likely to exist for 2 reasons. First, as noted above, I believe that conditions in crop fields are probably going to be of lower quality than suggested by the data in Table 14. Second, sample sizes may have

limited my ability to detect any real differences. Thus, all other factors being equal, the conversion of crop fields to pine plantations is likely to benefit quail populations by providing more suitable nest/brood habitat conditions. This benefit however, will likely be lost 8-10 years after enrollment in the program because of canopy closure and the elimination of understory vegetation capable of providing food and cover for the bobwhite.

Without question, the long-term effects of the retiring cropland into the CRP and converting these sites to pines is going to negatively impact quail populations throughout Halifax County. CP3 stands over 8 years-of-age and those receiving some level of commercial thinning, provided virtually no suitable nest/brood habitat. These findings nearly duplicate the predictions of Stauffer et al. (1990). These researchers used a multiple regression model (Cline 1989) relating an index of quail abundance to land use types and other attributes of the agricultural landscape, to predict the likely response of quail to various land use change scenarios that might accompany the CRP. Although the model did not contain coverage variables for CRP practices, the authors were able to adapt the model by assuming the variable "area of young (8-15 years-old) pine plantations" could be used as a surrogate for CP3 stands > 8 years-of-age. That they found a significant negative response by quail to increases in this surrogate measure for CP3 > 8 years-old, suggests that the

assumption was valid, given the findings from the present study. The results from this earlier study, as well as those from the present investigation, strongly suggest that converting cropfields to pines is likely to have a net negative impact on quail, despite potential initial short-term benefits.

Stauffer et al. (1990) cautioned readers against using the results of their investigation as a standard. The authors noted that, although they felt the results were relatively sound, there were several factors that limited the generalizability of the study's findings. First, the model used in their simulations was able to account for just under 50% of the variation in the index of quail abundance. In addition, the authors acknowledged that their model did not consider the spatial relationships among the various habitat components, an extremely relevant factor when managing quail habitat. This factor was not considered in the present study either. However, in Chapter 1, I attempted to demonstrate that spatial relations of habitat type, i.e., interspersed, was not limiting quail populations. Nor was winter food or cover. Rather, it was a shortage of nest/brood habitat. Thus, under the present conditions, it seems as though "where" is not nearly as relevant as how much. The addition of nest/brood habitat to the landscape should, at least in the short term, positively impact quail populations. There may be some loss of winter food with the conversions and some reduction in habitat diversity as well. However, these changes

should be insignificant, at least until the changes alter the conditions to such an extent that another factor other than nest/brood habitat becomes limiting. In conclusion, I believe that the conversion of crop fields to CP1 and CP3 sites will benefit quail in the short term, regardless of where the changes take place. However, in those locations where pines are planted, we can expect to see conditions for quail begin to deteriorate at about 8 years after the pines are planted.

CHAPTER 3: MICRO-HABITAT USE WITHIN THE COVEY HOME RANGE

INTRODUCTION

Species respond to their habitat differently at different scales. The previous chapter and earlier work by O'Neil (1993) suggest that the HSI model for the northern bobwhite can provide managers with a reasonable estimate of the species' response to habitat alterations brought about as a result of large scale land developments. The model was designed for application at such a scale. As a result, using the model to guide local (small-scale) habitat improvements and predict the effects of habitat alterations may yield unexpected results. In light of this, we embarked on an evaluation of the factors that may influence habitat use within the covey home range. Our specific objective was to test the null hypothesis that habitat use within a covey's home range was independent of 7 habitat components. Six of these habitat components, including percent canopy cover of herbaceous vegetation, % of herbaceous canopy that is grass, percent bare ground, percent canopy cover of herbaceous quail foods, percent woody vegetation < 2 m, and vegetation height, are used in the northern bobwhite HSI model. In addition, I estimated the percent canopy cover of honeysuckle.

METHODS

Trapping and Monitoring

We trapped quail with baited funnel traps during January-early March 1990 and 1991 (Stoddard 1931). Birds were sexed, aged, weighed, and fitted with 6-g bib-mounted radio-transmitters (Holohill Inc., Ontario, Canada). Sixty-six birds representing 12 coveys from 8 sites were radio-tagged during the 2-year study. We monitored 19 birds in 4 coveys in 1990 and 47 birds in 8 coveys in 1991. An average of 5.5 birds was radio-tagged per covey with a range of 3-11.

Vegetation Sampling and Analysis

Radio locations were compiled for each covey and a generalized home range estimated by delineating the outermost locations. Extreme outliers were excluded. Because our goal was to determine what factors influenced micro-habitat selection within the covey home range, we initially chose to sample the vegetation at individual radio locations and compare these data to that collected at unused sites of comparable size within the home range. However, because single radio locations are nearly instantaneous observations, we chose to sample the vegetation within a plot centered on multiple observations (radio locations per vegetation plot varied from 5 to 18, Fig. 31). We sampled the vegetation within a 35-m radius circular plot. This

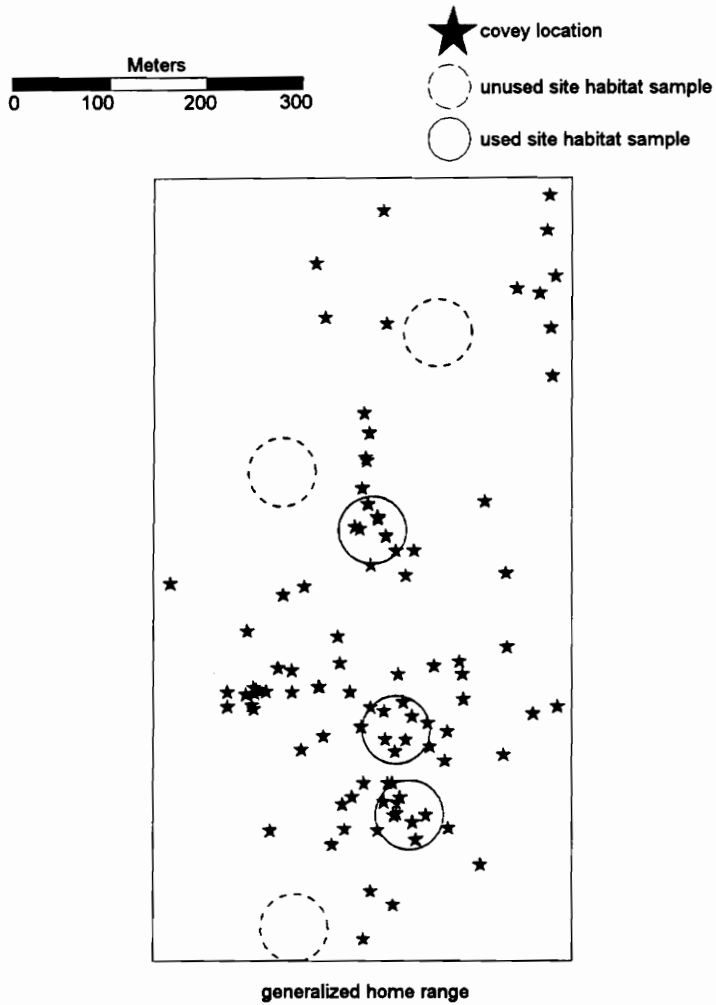


Figure 31. Sampling protocol used to compare micro-habitat conditions at used and unused sites within 12 northern bobwhite covey home ranges. Home range estimates and use sites are based on radio telemetry data collected January to July, 1990 and 1991, Halifax County, Virginia.

plot size represented a compromise between the density of locations within the plot and required sampling time. We attempted to sample those sites with the greatest density of locations. For those sites with an equal number of observations, we randomly selected a site. We sampled vegetation at 3 use sites within each home range. Use sites did not encompass all radio locations within the home range and did not overlap each other. Point sampling (Hays et al. 1981) was used to generate canopy cover estimates for herbaceous cover, woody vegetation < 2 m tall, honeysuckle, proportion of the herbaceous canopy represented by grasses, and herbaceous quail foods and the amount of bare or lightly-littered ground. A graduated dowel was used to estimate herbaceous vegetation height. All measurements were taken at 1-m intervals along 2 70-m transects bisecting the plot in the cardinal directions. We randomly selected 3 sites of equal size from the unused portion of the home range and sampled these in an identical manner.

Means for the 7 habitat variables were computed for each home range by first pooling over the 2 transects within each site and then pooling site means. Distributions for all variables were not normally distributed. All analyses were based on the sample of 12 covey home ranges.

Differences in means between used and unused sites for each of the 12 home ranges were generated for each of the 7 habitat variables. A signed-rank (Statistix

1991) test was used to test the hypothesis that the mean difference between the used and unused samples was 0. We also used simple linear regression (SAS 1985) to test the null hypothesis that habitat selection within the home range was not occurring. We regressed means for the 7 habitat variables from used sites on the means from unused sites and tested the resulting slopes to determine if they differed from 1 (Dodge et al. 1990).

RESULTS

Analyses were based on a total of 986 independent radio locations collected from mid-January to July 1990 ($N = 605$) and mid-January to mid-March 1991 ($N = 381$). Except for occasions when a covey was scattered, the sampling unit was the covey, not individual birds. We averaged 151 observations (range: 60-306) per covey in 1990 and 48 (range: 19-84) in 1991. We located coveys an average of 8 times weekly. Telemetry data were collected from 0500-1930 hours. Except for the period from 1800-1930 hours (which represented approximately 7% of all locations), results indicated that observations were nearly equally distributed in 3 hour periods from approximately 0530-1800 hours. Sixty-one observations represented nocturnal roost sites.

The Wilcoxon signed-rank tests yielded no differences ($P < 0.05$) in means for any of the 7 habitat variables except canopy cover of herbaceous quail foods

($\Sigma=66$, $P = 0.04$). Mean percent cover of herbaceous quail foods at used and unused sites was 18.5 and 14.9%, respectively (Table 15). Used sites tended to have more bare ground, grass, and woody vegetation <2 m tall than unused sites, but generally less honeysuckle and total herbaceous vegetation. Herbaceous vegetation height tended to be lower at used sites ($\bar{x} = 14.2$ vs. 16.3 cm).

Under the null hypothesis (i.e., no preferential use of habitat within the home range) mean values for each of the habitat variables estimated should be similar for both used and unused sites. Thus, plotting used vs. unused data pairs should generate a curve with a slope not significantly different from 1 and an intercept of 0 (Dodge et al. 1990). Except for woody vegetation <2 m tall, all slopes tested differed (honeysuckle, $P = 0.04$; all others $P < 0.01$) from 1 and all intercepts from 0, suggesting that use was not random with respect to these parameters (Table 15, Fig. 32). As with the signed-rank test, the regression analysis suggests that, at least for the range of conditions sampled, the amount of woody vegetation <2 m tall had little impact on habitat use during the period examined.

Although we found that the amount of bare ground within the home range varied from 30 to 100%, areas consistently used by quail had $\geq 61\%$ bare ground. Only in cases where bare ground at unused sites within the home range averaged between 65 and 85% did we find quail using habitats as predicted under the null

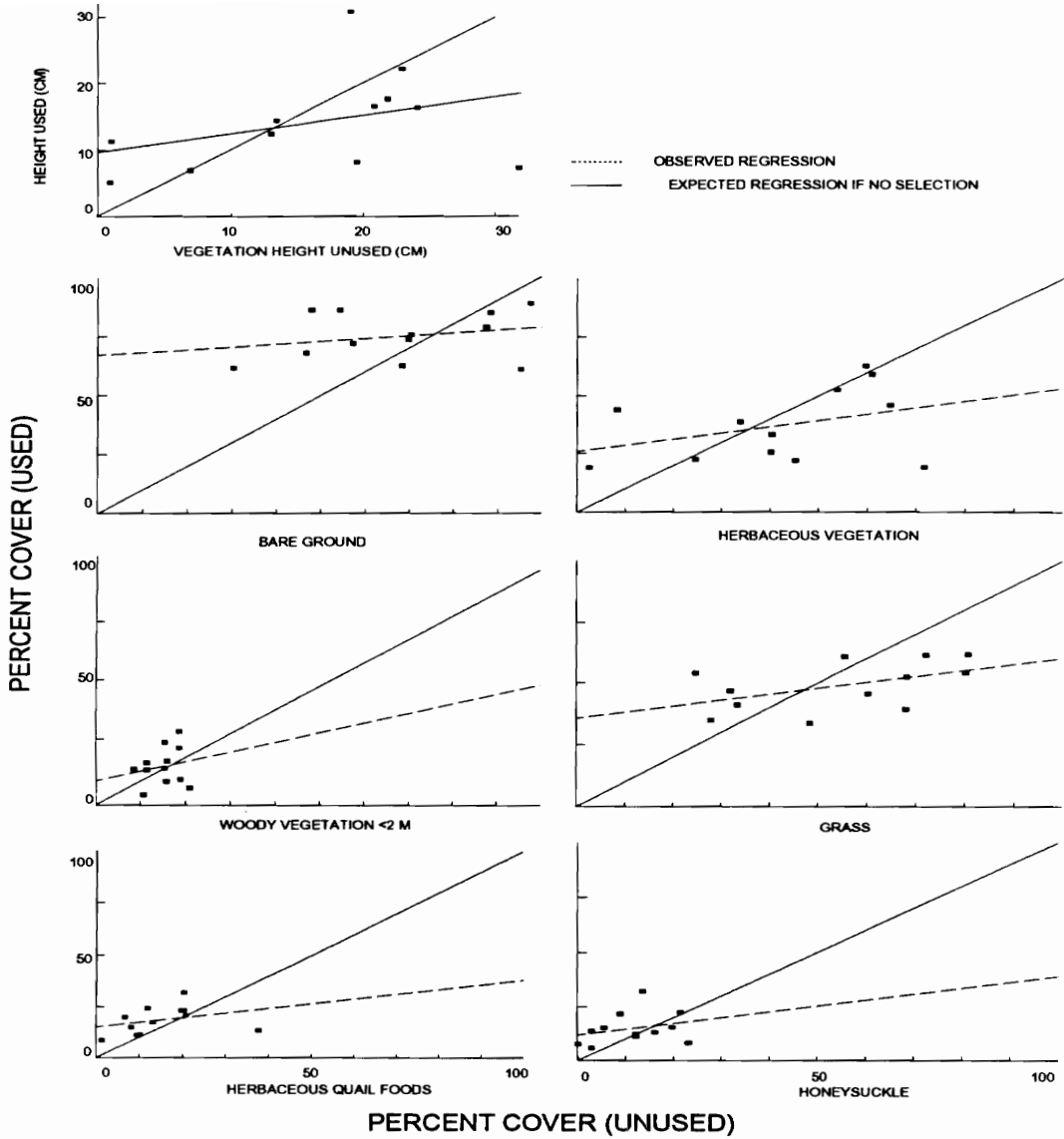


Figure 32. Regressions of means of 7 habitat variables estimated at used sites on means from corresponding unused sites within the home ranges of 12 coveys of northern bobwhite, Halifax County, VA, 1990-91. Under the null hypothesis of no selection, a line with a slope of 1 and intercept of 0 is expected.

Table 15. Analysis of northern bobwhite habitat selection, Halifax County, Virginia, 1990-91. Signed-rank tests of 7 micro-habitat measurements from used and unused sites within 12 home ranges and a simple linear regression of means for each variable from used sites on corresponding means from unused sites, were used to test the null hypothesis of no selection.

Variable	Wilcoxon signed-rank						Regression					
	Used			Unused			P^b			β_0^e		
	\bar{x}	SE	Σ^{+a}	\bar{x}	SE	Σ^{+a}	P^b	β_1^c	P^d	β_0^e	P^f	
Bare or lightly -littered ground	75.3	2.9	52	67.7	6.2	52	0.33	0.12	<0.01	67.0	<0.01	
Honeysuckle	14.9	2.2	54	11.5	2.2	54	0.26	0.28	0.04	11.7	0.02	
Percent of herbaceous canopy that is grass	48.9	2.9	25	54.2	5.9	25	0.29	0.24	<0.01	35.7	<0.01	
Herbaceous quail foods	18.5	2.0	66	14.9	2.7	66	0.04	0.23	<0.01	15.0	<0.01	
Woody vegetation <2 m	16.3	2.3	45	15.1	1.1	45	0.67	0.42	0.38	9.9	0.34	
Herbaceous vegetation height (cm)	14.2	2.1	32	16.3	2.7	32	0.61	0.28	<0.01	9.7	0.05	
Herbaceous vegetation	37.1	4.6	28	42.2	6.3	28	0.41	0.27	<0.01	25.8	0.03	

^aSigned-rank statistic.

^bSignificance of 2-tailed signed-rank test.

^cSlope of regression. Slopes differing significantly from 1 indicate selection.

^dProbability of $\beta_1 = 1$.

^eIntercept of regression line.

^fProbability of $\beta_0 = 0$.

hypothesis that conditions at used sites should be similar to those at unused sites when there is no selection occurring. Observations deviated considerably from the prediction line outside the 68-85% range (Fig. 32). When unused sites within the home range averaged <20% canopy cover of quail foods, quail tended to select sites that provided more food than what would have been found had use been random. For honeysuckle, we found that when unused sites within the home range averaged from 0-10%, used sites fell above the prediction line. However, when unused conditions ranged from about 12-25%, the points fell very close to the predicted line. For percent of the herbaceous canopy that is grasses, we found that used sites fell above the prediction line when unused levels < 40%, and were below this line where cover at unused sites was > 50%. We found little if any noticeable pattern in the data for total herbaceous cover and herbaceous vegetation height (Fig. 32). For most of the range sampled, we had sites both above and below the prediction line.

DISCUSSION

We compared data for 7 habitat variables collected at used and unused sites within the home ranges of 12 coveys to assess the dependency between these 7 habitat parameters and overall habitat suitability. We assumed that use was an indicator of quality. Our data suggested that the distribution of radio locations within

the 12 home ranges was partly influenced by 6 of the 7 variables estimated. Except for herbaceous quail foods, no differences in means between used and unused sites were detected. For several of the variables, we attribute this partly to the disparity in the variances between the used and unused samples. Although homogeneity of variances is not an assumption of the signed-rank test, large differences in variances may limit the power of this test. The availability of bare or lightly-littered ground clearly influenced habitat use within the home ranges examined. The importance of bare ground has been both qualitatively and quantitatively described elsewhere. Stoddard (1931) described ideal foraging conditions as areas with open vegetation interspersed with some bare ground. Abandoned agricultural fields and croplands with rough stubble have been shown to be suitable sources of bobwhite food (Ellis et al. 1969). Workers in West Virginia found a negative ($P < 0.05$) correlation between the percent ground cover and feeding rates for broods (Brown and Samuel 1978). More recently, Burger et al. (1990) noted the potential of CRP fields in Missouri to provide optimal brood foraging habitat due to the presence of bare ground at these sites. Additionally, studies of bobwhite roosting habits (Klimstra and Zicarrdi 1963, Ellis et al. 1969) found bare or lightly-littered ground to be a consistent feature of roost sites examined.

Although the HSI model for the northern bobwhite does not identify

honeysuckle as a critical habitat component, we chose to quantify its availability because of its prevalence on the study area. We found that when available conditions averaged < 10% cover of honeysuckle, quail tended to use sites with more honeysuckle than was generally available, suggesting that habitat quality may be improved by the presence of honeysuckle, up to a certain point. Because daily observations were collected over a 12-hour period, it would be speculation to suggest that this affinity for honeysuckle was the result of a single factor. Based on earlier work and personal observation, it is likely that sites with honeysuckle were used as loafing, protective, and roosting cover. Roseberry and Klimstra (1984) noted that Japanese honeysuckle (*L. japonica*) was frequently an understory component of woody headquarters of coveys in Illinois. Yoho and Dimmick (1972) noted the consistency with which covey activity centers in Tennessee were characterized by honeysuckle. Further, they reported that 63 of 107 roosts were located in honeysuckle.

From the regression analysis and the signed-rank test, it is apparent that habitat use within the home range varied with food availability, within the range of conditions examined. For nearly 70% of the observations, quail selected sites with more food than what was generally available within the home range. Except as presented in the HSI model for the bobwhite (Schroeder 1985), precise quantitative

data on this variable are lacking.

Patches of woody vegetation < 2 m in height are presumed to provide protective cover for the bobwhite (Schroeder 1985). That we found the slope not differing significantly from 1 nor the intercept from 0 suggests that habitat use within the home range varies independently of this parameter. The disparity between our conclusions and those of Schroeder (1985) may be a function of scale. Cover needs of the bobwhite are rarely quantitatively described, and have been qualitatively described as dense shrubby thickets providing refuge from both predators and the sun (Rosene 1969). Davis (1964) described those sites providing dense woody vegetation > 1 m tall as escape cover. Although our data included midday observations, it is possible that the number of relocations during that period of the day when coveys are purportedly using cover conditions as described, was limited, and thus we were unable to detect any significant use of these conditions. We more frequently observed birds using wooded areas in later successional, pole and mixed pole-saw timber stages as escape cover rather than early successional stages as described above. Perhaps we would have detected a preference for conditions more closely aligned with those described in the model had we sampled the home range more intensively and compared conditions to those outside the home range.

Herbaceous vegetation height, total herbaceous cover, and the percent of the herbaceous canopy that is grass, appeared to have some influence on winter habitat use. Caution is warranted when interpreting these findings. We found the rank correlations between these 3 variables and the amount of bare or lightly-littered ground to be quite high ($r = 0.88, 0.66, \text{ and } 0.77, P < 0.05$, for grass, herbaceous cover, and vegetation height, respectively). Thus, it is possible that demonstrated association between winter habitat use and herbaceous vegetation height, total herbaceous cover, and the percent of the herbaceous canopy that is grass may be an artifact of the data resulting from the correlations between these 3 variables and the amount of bare or lightly littered ground within the home ranges.

The temporal and spatial distributions of many species are the result of habitat selection at various scales. Many times, the factors that influence selection vary with the scale of investigation. Our study addressed those factors that influence selection within the home range. The 7 variables we quantified did not entirely account for the distribution of radio locations, suggesting that other factors are undoubtedly operating. However, because of the large amount of variation within the home ranges relative to the "core areas," it may be advantageous to consider focusing future management activities on core areas instead of home ranges. Although we have no data on how the variation within the home range compares to

that outside its boundaries, the observed variation within the home range may be an indication that use of an area is more a function of the availability of 2-3 core areas than "average" conditions over the respective site.

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APPENDICES

Appendix Table 1. Equivalent percent of station providing optimum winter food, cover, and nest/brood habitat and their associated Suitability Indices for 121 stations sampled 1986-1991, Halifax County, Virginia.

Station	Equivalent Percent of Station in Optimum Condition						Limiting life requisite
	Winter food	SI	Cover	SI	Nest/brood	SI	
23	62.4	0.78	11.4	0.57	28.6	1.00	cover
96	31.2	0.39	6.7	0.34	28.6	1.00	cover
97	40.7	0.51	8.0	0.40	22.4	1.00	cover
1	36.3	0.45	23.3	1.00	11.1	1.00	food
2	35.8	0.45	22.6	1.00	15.0	1.00	food
3	31.0	0.39	16.7	0.84	14.3	1.00	food
4	37.2	0.46	34.3	1.00	13.4	1.00	food
5	34.2	0.43	28.8	1.00	7.1	0.71	food
6	33.9	0.42	40.7	1.00	6.9	0.69	food
7	32.4	0.41	20.8	1.00	18.7	1.00	food
8	41.6	0.52	14.3	0.72	23.3	1.00	food
9	40.4	0.50	11.7	0.58	22.5	1.00	food
10	43.2	0.54	11.8	0.59	21.7	1.00	food
11	28.7	0.35	20.6	1.00	23.9	1.00	food
12	48.4	0.61	12.2	0.61	25.0	1.00	food
13	7.7	0.10	6.5	0.32	33.7	1.00	food
14	8.9	0.11	5.6	0.28	33.7	1.00	food
15	4.8	0.06	6.1	0.30	33.7	1.00	food
16	19.1	0.24	23.5	1.00	13.9	1.00	food
17	32.2	0.40	24.5	1.00	11.5	1.00	food
18	14.3	0.18	32.0	1.00	12.3	1.00	food
19	15.8	0.20	17.1	0.85	22.1	1.00	food
20	35.9	0.45	20.1	1.00	11.7	1.00	food
21	29.4	0.37	25.3	1.00	10.3	0.99	food
22	28.1	0.35	30.2	1.00	3.9	0.39	food
24	26.3	0.33	30.8	1.00	4.3	0.43	food

Appendix Table 1. Continued.

Station	Equivalent Percent of Station in Optimum Condition						Limiting life requisite
	Winter food	SI	Cover	SI	Nest/brood	SI	
25	28.4	0.36	14.6	0.73	21.3	1.00	food
26	25.5	0.32	18.4	0.92	9.9	1.00	food
27	34.5	0.43	26.7	1.00	11.5	1.00	food
28	38.0	0.48	20.3	1.00	19.5	1.00	food
29	36.8	0.46	16.0	0.80	18.2	1.00	food
30	23.3	0.29	20.5	1.00	17.6	1.00	food
31	41.5	0.52	22.3	1.00	12.8	1.00	food
32	36.6	0.46	22.9	1.00	12.7	1.00	food
33	38.7	0.48	27.2	1.00	8.4	0.84	food
34	37.0	0.46	23.6	1.00	14.2	1.00	food
35	24.7	0.31	17.5	0.87	29.4	1.00	food
36	33.0	0.41	21.8	1.00	8.7	0.87	food
37	34.9	0.44	23.4	1.00	12.1	1.00	food
38	33.2	0.41	29.9	1.00	19.3	1.00	food
39	42.3	0.53	24.6	1.00	16.2	1.00	food
40	33.8	0.42	24.8	1.00	13.3	1.00	food
41	46.6	0.58	28.8	1.00	17.6	1.00	food
42	24.4	0.31	21.3	1.00	27.0	1.00	food
43	34.4	0.43	17.4	0.87	14.9	1.00	food
44	23.7	0.30	23.5	1.00	7.9	0.79	food
45	10.0	0.13	12.8	0.64	28.5	1.00	food
46	9.3	0.12	12.9	0.64	29.7	1.00	food
47	20.0	0.25	10.1	0.50	28.4	1.00	food
48	22.3	0.28	21.9	1.00	12.9	1.00	food
49	34.3	0.43	24.9	1.00	8.8	0.88	food
50	33.9	0.42	21.9	1.00	17.9	1.00	food
51	38.9	0.49	26.7	1.00	13.9	1.00	food

Appendix Table 1. Continued.

Station	Equivalent Percent of Station in Optimum Condition						Limiting life requisite
	Winter food	SI	Cover	SI	Nest/brood	SI	
52	22.5	0.28	29.8	1.00	5.8	0.58	food
53	44.3	0.55	34.4	1.00	12.8	1.00	food
54	10.3	0.12	12.7	0.63	32.4	1.00	food
55	6.4	0.08	7.5	0.38	34.0	1.00	food
56	10.6	0.13	8.2	0.41	32.5	1.00	food
57	6.7	0.08	2.7	0.13	38.2	1.00	food
58	28.2	0.35	25.1	1.00	13.8	1.00	food
59	39.9	0.50	26.1	1.00	11.6	1.00	food
60	17.1	0.21	18.9	0.94	18.8	1.00	food
61	26.8	0.33	18.5	0.92	11.1	1.00	food
62	25.0	0.31	29.5	1.00	6.8	0.68	food
63	30.0	0.38	24.5	1.00	18.5	1.00	food
64	28.9	0.36	23.0	1.00	17.1	1.00	food
65	25.5	0.32	16.0	0.80	20.9	1.00	food
66	11.6	0.14	5.6	0.28	28.5	1.00	food
67	32.2	0.40	18.2	0.91	14.3	1.00	food
68	34.3	0.43	22.9	1.00	12.0	1.00	food
69	30.4	0.38	27.6	1.00	5.1	0.51	food
70	42.1	0.53	19.8	0.99	12.3	1.00	food
71	38.2	0.48	18.1	0.89	14.8	1.00	food
72	38.1	0.48	13.0	0.64	19.1	1.00	food
73	28.8	0.36	27.8	1.00	6.2	0.62	food
74	39.8	0.50	17.2	0.86	18.8	1.00	food
75	40.9	0.51	20.2	1.00	15.5	1.00	food
76	43.7	0.55	26.3	1.00	22.1	1.00	food
77	40.6	0.51	20.6	1.00	16.7	1.00	food

Appendix Table 1. Continued.

Station	Equivalent Percent of Station in Optimum Condition						Limiting life requisite
	Winter food	SI	Cover	SI	Nest/brood	SI	
78	43.1	0.54	14.4	0.72	22.8	1.00	food
79	38.5	0.48	15.4	0.77	17.9	1.00	food
80	45.5	0.57	21.1	1.00	18.1	1.00	food
81	41.4	0.52	33.5	1.00	18.3	1.00	food
82	39.3	0.49	31.0	1.00	18.4	1.00	food
83	16.4	0.20	15.2	0.72	22.2	1.00	food
84	20.3	0.25	14.1	0.70	17.8	1.00	food
85	39.2	0.49	25.6	1.00	16.0	1.00	food
86	37.9	0.47	17.8	0.84	22.1	1.00	food
87	17.6	0.22	20.5	1.00	18.6	1.00	food
88	19.7	0.25	18.0	0.90	18.8	1.00	food
89	30.0	0.37	28.7	1.00	8.3	0.83	food
90	29.6	0.37	31.2	1.00	9.7	0.89	food
91	35.8	0.45	31.1	1.00	16.9	1.00	food
92	35.3	0.44	23.7	1.00	9.9	0.97	food
93	48.7	0.61	25.2	1.00	19.3	1.00	food
94	38.7	0.48	11.8	0.59	22.5	1.00	food
95	15.1	0.19	13.4	0.67	17.9	1.00	food
98	26.8	0.33	25.7	1.00	11.3	1.00	food
99	27.7	0.35	43.7	1.00	10.3	1.00	food
100	33.2	0.42	39.4	1.00	6.0	0.60	food
102	27.5	0.34	32.9	1.00	3.0	0.39	nest
103	26.4	0.33	39.7	1.00	6.3	0.63	food
104	39.1	0.49	26.3	1.00	8.9	0.89	food
106	35.3	0.44	28.3	1.00	9.0	0.90	food
107	35.3	0.44	24.3	1.00	10.3	1.00	food
108	40.9	0.51	21.7	1.00	15.2	1.00	food

Appendix Table 1. Continued.

Station	Equivalent Percent of Station in Optimum Condition						Limiting life requisite
	Winter food	SI	Cover	SI	Nest/brood	SI	
109	27.0	0.34	30.0	1.00	8.5	0.85	food
110	30.4	0.38	14.3	0.71	21.8	1.00	food
111	34.5	0.43	23.8	1.00	12.2	1.00	food
112	31.4	0.39	34.1	1.00	4.2	0.42	food
113	26.8	0.34	37.0	1.00	9.2	0.92	food
114	32.7	0.41	20.4	1.00	16.1	1.00	food
115	33.3	0.42	27.4	1.00	12.2	1.00	food
117	33.8	0.42	29.2	1.00	10.8	1.00	food
118	42.8	0.53	17.0	0.85	15.7	1.00	food
119	40.0	0.50	20.8	1.00	16.2	1.00	food
120	19.2	0.24	36.4	1.00	12.9	1.00	food
121	22.1	0.28	41.3	1.00	15.3	1.00	food
101	26.5	0.33	35.6	1.00	1.4	0.14	nest
105	28.2	0.35	30.8	1.00	2.9	0.29	nest
116	27.1	0.34	37.3	1.00	2.3	0.23	nest

Appendix Table 2. Common and scientific names of food plants considered to be locally preferred quail food items, Halifax County, Virginia. Data are from Landers and Johnson's (1976) list of major food items of northern bobwhite in the Piedmont physiographic province of the Southeastern United States.

Common name	Scientific name
Ash	<i>Fraxinus</i> spp.
Beggar weeds	<i>Desmodium</i> spp.
Beggarticks	<i>Bidens</i> spp.
Bicolor lespedza	<i>Lespedeza bicolor</i>
Black locust	<i>Robinia pseudoacacia</i>
Blackberries	<i>Rubus</i> spp.
Bull grass	<i>Panicum boscianum</i>
Bush clovers	<i>Lespedeza</i> spp.
Common lespedza	<i>Lespedeza striata</i>
Corn	<i>Zea mays</i>
Cowpeas	<i>Vigna</i> spp.
Crab grass	<i>Digitaria</i> spp.
Cranesbill	<i>Geranium</i> spp.
Dogwoods	<i>Cornus</i> spp.
Dove weeds	<i>Croton</i> spp.
Foxtail grass	<i>Setaria</i> spp.
Grapes	<i>Vitis</i> spp.
Ground nut	<i>Apios americana</i>
Hog peanut	<i>Amphicarpa bracteata</i>
Honeysuckles	<i>Lonicera</i> spp.
Jewel weeds	<i>Impatiens</i> spp.
Johnson grass	<i>Sorghum halepense</i>
Korean clover	<i>Lespedeza stipulacea</i>
Milk peas	<i>Galactia</i> spp.
Night shades	<i>Solanum</i> spp.
Nut rushes	<i>Scleria</i> spp.
Oaks	<i>Quercus</i> spp.

Appendix Table 2. Continued.

Common name	Scientific name
Panic grass	<i>Panicum</i> spp.
Partridge peas	<i>Cassia</i> spp.
Paspalums	<i>Paspalums</i> spp.
Pines	<i>Pinus</i> spp.
Poor Joe	<i>Diodia teres</i>
Ragweeds	<i>Ambrosia</i> spp.
Sassafras	<i>Sassafras</i> spp.
Sericea	<i>Lespedeza cuneata</i>
Smartweeds	<i>Polygonum</i> spp.
Sorghum	<i>Sorghum vulgare</i>
Soybeans	<i>Glycine max</i>
Spurred butterfly peas	<i>Centrosema virginianum</i>
Sumacs	<i>Rhus</i> spp.
Sweet gum	<i>Liquidambar styraciflua</i>
Vetches	<i>Vicia</i> spp.
Wheat	<i>Triticum</i> spp.
Wildbeans	<i>Strophostyles</i> spp.
Wood sorrels	<i>Oxalis</i> spp.

Appendix Table 3. Exploratory analyses used in the field evaluation of the northern bobwhite Habitat Suitability Index model. An index of relative quail abundance was used in all analyses. All analyses were run at the transect ($n = 10$) and station ($n = 121$) levels.

Model variable	Analysis
Equivalent optimum nest/brood habitat	Only those habitats with a nest/brood LRSI > 0.3 contributed to the estimate of available nest/brood habitat.
Equivalent optimum nest/brood habitat	Eight habitats (grazed saplings/light stocking; grazed cutovers with saplings/light stocking; grazed saplings/heavy stocking; saplings/light stocking; saplings, poles and mature light stocking; cutovers with saplings/medium stocking, poles/light stocking; saplings/heavy stocking; saplings and poles/medium stocking, mature/light stocking) initially included in the estimate of available nest/brood habitat were excluded. Two habitats (saplings/light stocking, poles/medium stocking; saplings and poles/medium stocking) initially excluded from the estimate of available nest/brood habitat, were added.
Equivalent optimum nest/brood habitat	Eight habitats (grazed saplings/light stocking; grazed cutovers with saplings/light stocking; grazed saplings/heavy stocking; saplings/light stocking; saplings, poles and mature light stocking; cutovers with saplings/medium stocking, poles/light stocking; saplings/heavy stocking; saplings and poles/medium stocking, mature/light stocking) initially included in the estimate of available nest/brood habitat, were excluded.
Equivalent optimum nest/brood habitat	Eight habitats (grazed saplings/light stocking; grazed cutovers with saplings/light stocking; grazed saplings/heavy stocking; saplings/light stocking; saplings, poles and mature light stocking; cutovers with saplings/medium stocking, poles/light stocking; saplings/heavy stocking; saplings and poles/medium stocking, mature/light stocking) initially included in the estimate of available nest/brood habitat were excluded. Two habitats (saplings/light stocking, poles/medium stocking; saplings and poles/medium stocking) initially excluded from the estimate of available nest/brood habitat, were added. Only those habitats with a nest/brood LRSI > 0.3 contributed to the estimate of available nest/brood habitat.
Equivalent optimum nest/brood habitat	Eight habitats (grazed saplings/light stocking; grazed cutovers with saplings/light stocking; grazed saplings/heavy stocking; saplings/light stocking; saplings, poles and mature light stocking; cutovers with saplings/medium stocking, poles/light stocking; saplings/heavy stocking; saplings and poles/medium stocking, mature/light stocking) initially included in the estimate of available nest/brood habitat were excluded. Two habitats (saplings/light stocking, poles/medium stocking; saplings and poles/medium stocking) initially excluded from the estimate of available nest/brood habitat, were added. Only those habitats with a nest/brood LRSI > 0.4 contributed to the estimate of available nest/brood habitat.
Equivalent optimum nest/brood habitat	Eight habitats (grazed saplings/light stocking; grazed cutovers with saplings/light stocking; grazed saplings/heavy stocking; saplings/light stocking; saplings, poles and mature light stocking; cutovers with saplings/medium stocking, poles/light stocking; saplings/heavy stocking; saplings and poles/medium stocking, mature/light stocking) initially contributing to the estimate of available nest/brood habitat were excluded. Two habitats (saplings/light stocking, poles/medium stocking; saplings and poles/medium stocking) initially excluded from the estimate of available nest/brood habitat, were added. The nest/brood LRSI was equal to the smallest of the SIs for "percent herbaceous canopy cover", "percent of herbaceous canopy that is grass" and percent bare or lightly-littered ground."
Equivalent optimum nest/brood habitat	Eight habitats (grazed saplings/light stocking; grazed cutovers with saplings/light stocking; grazed saplings/heavy stocking; saplings/light stocking; saplings, poles and mature light stocking; cutovers with saplings/medium stocking, poles/light stocking; saplings/heavy stocking; saplings and poles/medium stocking, mature/light stocking) initially included in the estimate of available nest/brood habitat, were excluded. Two habitats (saplings/light stocking, poles/medium stocking; saplings and poles/medium stocking) initially excluded from the estimate of available nest/brood habitat, were added. The nest/brood LRSI was equal to the SI for "percent bare or lightly-littered ground."

Appendix Table 3. Continued.

Model variable	Analysis
Equivalent optimum nest/brood habitat	Eight habitats (grazed saplings/light stocking; grazed cutovers with saplings/light stocking; grazed saplings/heavy stocking; saplings/light stocking; saplings, poles and mature light stocking; cutovers with saplings/medium stocking; poles/light stocking; saplings/heavy stocking; saplings and poles/medium stocking; mature/light stocking) initially included in the estimate of available nest/brood habitat, were excluded. Two habitats (saplings/light stocking; poles/medium stocking; saplings and poles/medium stocking) initially excluded from the estimate of available nest/brood habitat, were added. The nest/brood LRSI was equal to the smallest of the SIs for "percent herbaceous canopy cover," "percent of herbaceous canopy that is grass," and "percent bare or lightly-littered ground." The habitat type "fallow crop field with saplings/light stocking," initially included in estimate of available nest/brood habitat, was excluded.
Equivalent optimum nest/brood habitat	Eight habitats (grazed saplings/light stocking; grazed cutovers with saplings/light stocking; grazed saplings/heavy stocking; saplings/light stocking; saplings, poles and mature light stocking; cutovers with saplings/medium stocking; poles/light stocking; saplings/heavy stocking; saplings and poles/medium stocking; mature/light stocking) initially included in the estimate of available nest/brood habitat, were excluded. The habitat type "saplings/light stocking, poles/medium stocking," initially excluded from the estimate of available nest/brood habitat, was added. The habitat type "fallow crop field with saplings/light stocking," initially included in estimate of available nest/brood habitat, was excluded.
Equivalent optimum nest/brood habitat	Initial group of habitats recommended by the HSI model. The nest/brood LRSI was equal to the geometric mean of the SIs for "percent of herbaceous canopy that is grass" and "percent bare or lightly-littered ground."
Equivalent optimum nest/brood habitat	Two habitats (saplings/light stocking, poles/medium stocking; saplings and poles medium stocking) initially excluded from the estimate of available nest/brood habitat, were added.
Equivalent optimum nest/brood habitat	The habitat type "saplings/heavy stocking," initially included in the estimate of available nest/brood habitat, was excluded.
Equivalent optimum nest/brood habitat	The habitat type "cutover with saplings/medium stocking, poles/light stocking," initially included in the estimate of available nest/brood habitat, was excluded.
Equivalent optimum nest/brood habitat	The habitat type "saplings, poles, and mature/light stocking," initially included in the estimate of available nest/brood habitat, was excluded.
Equivalent optimum nest/brood habitat	The habitat type "grazed saplings/light stocking," initially included in the estimate of available nest/brood habitat, was excluded.
Equivalent optimum nest/brood habitat	The habitat type "poles and mature/light stocking," initially included in the estimate of available nest/brood habitat, was excluded.

Appendix Table 3. Continued.

Model variable	Analysis
Equivalent optimum nest/brood habitat	The habitat type "saplings/light stocking," initially included in the estimate of available nest/brood habitat, was excluded.
Equivalent optimum nest/brood habitat	Initial group of habitats recommended by the HSI model. The nest/brood LRSI was equal to the SI for "percent bare or lightly-littered ground."
Equivalent optimum nest/brood habitat	Initial group of habitats recommended by the HSI model. The nest/brood LRSI was equal to the geometric mean of the SIs for "percent of herbaceous canopy that is grass" and "percent herbaceous canopy cover."
Equivalent optimum nest/brood habitat	Initial group of habitats recommended by the HSI model. The nest/brood LRSI was equal to the SI for "percent of herbaceous canopy that is grass."
Equivalent optimum nest/brood habitat	Initial group of habitats recommended by the HSI model. The nest/brood LRSI was equal to the SI for "percent herbaceous canopy cover."
Equivalent optimum nest/brood habitat	Initial group of habitats recommended by the HSI model. The nest/brood LRSI was equal to the geometric mean of the SIs for "percent herbaceous canopy cover" and "percent bare or lightly-littered ground."
Equivalent optimum winter food	Only those polygons with a winter food LRSI > 0.5 were included in the estimate of available winter food.
Equivalent optimum winter food	Ten habitat types (cutovers with saplings/light stocking; saplings, poles, and mature/light stocking; cutovers with saplings/medium stocking; poles/light stocking; saplings/heavy stocking; poles/medium stocking; grazed saplings/light stocking; poles/medium stocking; grazed saplings/heavy stocking; saplings/light stocking; poles and mature/light stocking; fallow crop fields with saplings/light stocking) initially included in the estimate of available winter food, were excluded. Pastures, initially excluded from the estimate of available winter food, were included.
Equivalent optimum winter food	Ten habitat types (cutovers with saplings/light stocking; saplings, poles, and mature/light stocking; cutovers with saplings/medium stocking; poles/light stocking; saplings/heavy stocking; poles/medium stocking; grazed saplings/light stocking; poles/medium stocking; grazed saplings/heavy stocking; saplings/light stocking; poles and mature/light stocking; fallow crop fields with saplings/light stocking) initially included in the estimate of available winter food, were excluded.
Equivalent optimum winter food	Initial group of habitats recommended by the HSI model. The SI for "density of mast producing trees" was used in place of the initial winter food LRSI for those habitats where mast was assumed to be available.
Equivalent optimum winter food	Five habitat types (cutovers with saplings/light stocking; saplings, poles, and mature/light stocking; cutovers with saplings/medium stocking; poles/light stocking; saplings/heavy stocking; poles/medium stocking) initially included in the estimate of available winter food, were excluded. Only those polygons with an estimated winter food LRSI > 0.5 contributed to the estimate of available winter food.

Appendix Table 3. Continued.

Model variable	Analysis
Equivalent optimum winter food	Five habitat types (cutovers with saplings/light stocking; saplings, poles, and mature/light stocking; cutovers with saplings/medium stocking, poles/light stocking; saplings/heavy stocking; poles/medium stocking) initially included in the estimate of available winter food, were excluded.
Equivalent optimum winter food	Initial group of habitats recommended by the HSI model. Only polygons with an estimated winter food LRSI > 0.4 contributed to the estimate of available winter food.
Equivalent optimum winter food	Initial group of habitats recommended by the HSI model. Only polygons with an estimated winter food LRSI > 0.6 contributed to the estimate of available winter food.
Equivalent optimum winter food	Initial group of habitats recommended by the HSI model. Two habitat types ("pasture" and "hayland") initially excluded from the estimate of available winter food, were included.
Equivalent optimum winter food	Initial group of habitats recommended by the HSI model. Only those stations where the index of quail abundance was ≤ 0.7 were used in the evaluation of the relationship between estimate available winter food and quail abundance.
Equivalent optimum winter food	Initial group of habitats recommended by the HSI model. Only those stations where the index of quail abundance was > 0.7 were used in the evaluation of the relationship between estimate available winter food and quail abundance.
Equivalent optimum winter food	Initial group of habitats recommended by the HSI model. Only those stations where the index of quail abundance was < 0.6 were used in the evaluation of the relationship between estimate available winter food and quail abundance.
Equivalent optimum winter food	Initial group of habitats recommended by the HSI model. Only those stations where the index of quail abundance was > 0.7 but < 1.1 were used in the evaluation of the relationship between estimate available winter food and quail abundance.
Equivalent optimum winter food	Initial group of habitats recommended by the HSI model. Only those stations where the index of quail abundance was > 0.6 but < 1.1 were used in the evaluation of the relationship between estimate available winter food and quail abundance.
Equivalent optimum winter food	Initial group of habitats recommended by the HSI model. Only those stations where the index of quail abundance was > 1.1 were used in the evaluation of the relationship between estimate available winter food and quail abundance.
Equivalent optimum winter food	Ten habitat types (cutovers with saplings/light stocking; saplings, poles, and mature/light stocking; cutovers with saplings/medium stocking, poles/light stocking; saplings/heavy stocking; poles/medium stocking; grazed saplings/light stocking, poles/medium stocking; grazed saplings/heavy stocking; saplings/light stocking; poles and mature/light stocking; fallow crop fields with saplings/light stocking) initially included in the estimate of available winter food, were excluded. Only those polygons with a winter food LRSI > 0.5 contributed to the estimate of available winter food.

Appendix Table 3. Continued.

Model variable	Analysis
Equivalent optimum winter food	Ten habitat types (cutovers with saplings/light stocking; saplings, poles, and mature/light stocking; cutovers with saplings/medium stocking, poles/light stocking; saplings/heavy stocking; poles/medium stocking; grazed saplings/light stocking, poles/medium stocking, grazed saplings/heavy stocking; saplings/light stocking; poles and mature/light stocking; fallow crop fields with saplings/light stocking) initially included in the estimate of available winter food, were excluded. The SI for "canopy cover of late winter quail foods" was used as the winter food LRSI for all habitat types contributing to the estimate of available winter food.
Equivalent optimum winter food	Ten habitat types (cutovers with saplings/light stocking; saplings, poles, and mature/light stocking; cutovers with saplings/medium stocking, poles/light stocking; saplings/heavy stocking; poles/medium stocking; grazed saplings/light stocking, poles/medium stocking; grazed saplings/heavy stocking; saplings/light stocking; poles and mature/light stocking; fallow crop fields with saplings/light stocking) initially included in the estimate of available winter food, were excluded. Two habitats (pasture and hayland) initially excluded from the estimate of available winter food, were included.
Equivalent optimum winter food	Initial group of habitats recommended by the model. Only those polygons with a winter food LRSI > 0.3 contributed to the estimate of available winter food.
Equivalent optimum winter food	Initial group of habitats recommended by the model. Only those polygons with a winter food LRSI > 0.3 contributed to the estimate of available winter food. The SI for "percent canopy cover of late-winter quail foods" was used as the winter food LRSI for all habitats.
Equivalent optimum winter food	Initial group of habitats recommended by the model. Only those polygons with a winter food LRSI > 0.4 contributed to the estimate of available winter food. The SI for "percent canopy cover of late-winter quail foods" was used as the winter food LRSI for all habitats.
Equivalent optimum winter food	Initial group of habitats recommended by the model. Only those polygons with a winter food LRSI > 0.5 contributed to the estimate of available winter food. The SI for "percent canopy cover of late-winter quail foods" was used as the winter food LRSI for all habitats.
Equivalent optimum winter food	Initial group of habitats recommended by the model. The SI for "percent canopy cover of late-winter quail foods" was used as the winter food LRSI for all habitats.
Equivalent optimum winter food	Ten habitat types (cutovers with saplings/light stocking; saplings, poles, and mature/light stocking; cutovers with saplings/medium stocking, poles/light stocking; saplings/heavy stocking; poles/medium stocking; grazed saplings/light stocking, poles/medium stocking; grazed saplings/heavy stocking; saplings/light stocking; poles and mature/light stocking; fallow crop fields with saplings/light stocking) initially included in the estimate of available winter food, were excluded. Only those polygons with a winter food LRSI > 0.4 contributed to the estimate of available winter food.
Equivalent optimum winter food	The contribution of mast to the estimate of available winter food was excluded for the 8 habitat types (grazed and ungrazed saplings, poles and mature/light stocking; grazed and ungrazed poles and mature/light stocking; grazed and ungrazed saplings and poles/medium stocking, mature light/stocking; grazed and ungrazed saplings/heavy stocking, poles and mature/light stocking) on the study area where mast was potentially available as a source of winter food.
Equivalent optimum winter food	For those habitats where estimated available winter food was based on LRSI ₁ (Fig. 5), LRSI ₂ was used in its place. All other habitats initially contributing to the estimate of available winter food were given a zero.

Appendix Table 3. Continued.

Model variable	Analysis
Equivalent optimum cover	Initial group of habitats recommended by the HSI model. Only those stations with an index of quail abundance > 0.6 and < 1.1 were used in the evaluation of the relationship between estimated available cover and quail abundance.
Equivalent optimum cover	Initial group of habitat types recommended by the HSI model. Only those stations with an index of quail abundance > 1.6 were used in the evaluation of the relationship between estimated available cover and quail abundance.
Equivalent optimum cover	All habitat types on the study area were assumed capable of providing cover at some level > 0 .
Equivalent optimum cover	All habitat types on the study area were assumed capable of providing cover at some level > 0 . Only those stations where the index of quail abundance was > 0.4 were used in the evaluation of the relationship between estimated available cover and quail abundance.
Equivalent optimum cover	All habitat types on the study area were assumed capable of providing cover at some level > 0 . Only those stations where the index of quail abundance was > 1.6 were used in the evaluation of the relationship between estimated available cover and quail abundance.