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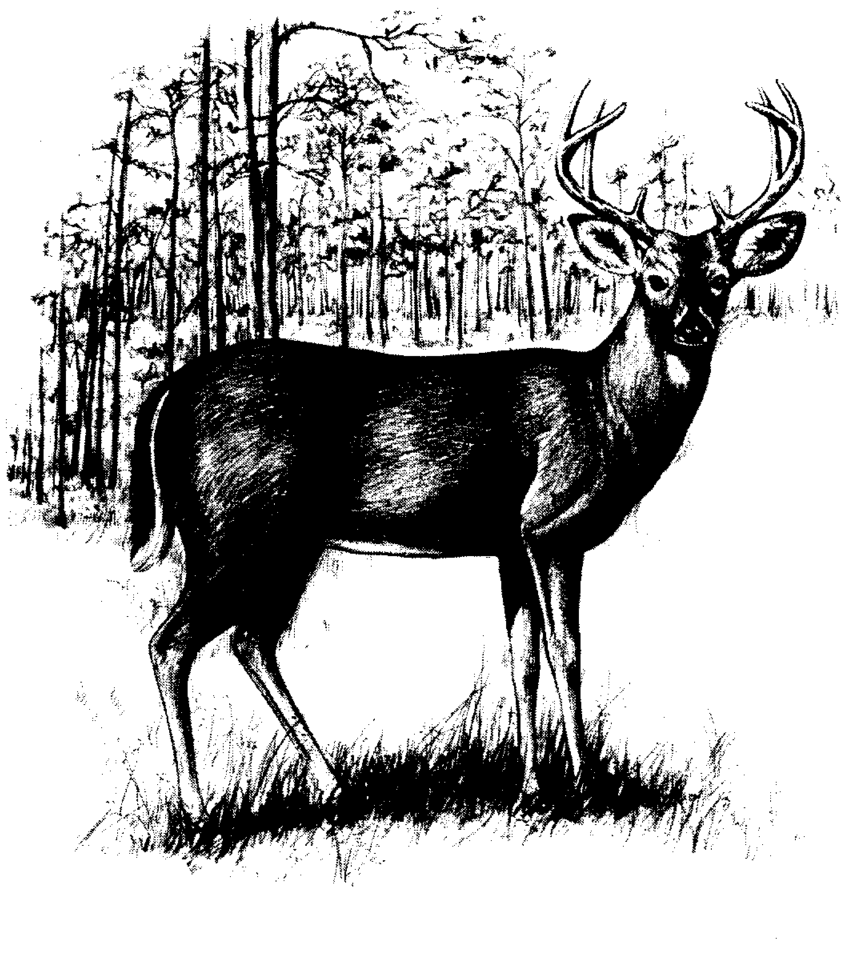

Fish and Wildlife Service

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HABITAT SUITABILITY INDEX MODELS: WHITE-TAILED DEER IN THE GULF OF MEXICO AND SOUTH ATLANTIC COASTAL PLAINS

by

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PREFACE

This document is part of the Habitat Suitability Index (HSI) Model Series [Biological Report 82(10)], which provides habitat information useful for impact assessment and habitat management. Several types of habitat information are provided. The Habitat Use Information section is largely constrained to those data that can be used to derive quantitative relationships between key environmental variables and habitat suitability. This information provides the foundation for the HSI model and may be useful in the development of other models more appropriate to specific assessment or evaluation needs.

The HSI Model section documents the habitat model and includes information pertinent to its application. The model synthesizes the habitat use information into a framework appropriate for field application and is scaled to produce an index value between 0.0 (unsuitable habitat) and 1.0 (optimum habitat). The HSI Model section includes information about the geographic range and seasonal application of the model, its current verification status, and a list of the model variables with recommended measurement techniques for each variable.

The model is a formalized synthesis of biological and habitat information published in the scientific literature and may include unpublished information reflecting the opinions of identified experts. Habitat information about wildlife species frequently is represented by scattered data sets collected during different seasons and years and from different sites throughout the range of a species. The model presents this broad data base in a formal, logical, and simplified manner. The assumptions necessary for organizing and synthesizing the species-habitat information into the model are discussed. The model should be regarded as a hypothesis of species-habitat relationships and not as a statement of proven cause and effect relationships. The model may have merit in planning wildlife habitat research studies about a species, as well as in providing an estimate of the relative quality of habitat for that species. User feedback concerning model improvements and other suggestions that may increase the utility and effectiveness of this habitat-based approach to fish and wildlife planning are encouraged. Please send suggestions to:

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CONTENTS

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WHITE-TAILED DEER (*Odocoileus virginianus*)
IN THE GULF OF MEXICO AND SOUTH ATLANTIC COASTAL PLAINS

HABITAT USE INFORMATION

General

Thirty subspecies of white-tailed deer have been identified as occurring throughout Central and North America (Baker 1984), where the species occurs on habitats varying in soil fertility, nutritional quality, and climatic extremes. The Habitat Suitability Index (HSI) models developed here are constructed for one portion of the deer's range - the Gulf of Mexico coastal plain. The models should also be relevant to the South Atlantic coastal plain, and concepts within the models may also be relevant to white-tailed deer habitats in other portions of their range. The data base from which these models were developed was largely compiled in east Texas and Louisiana, a subportion of the gulf coastal plain. Baker (1984) lists several recognizable subspecies of white-tailed deer occurring within the geographical area for which these models were developed. I make no distinctions between the requirements of subspecies of white-tailed deer in these habitat models.

Five major grassland and forest types occur within the South Atlantic and Gulf of Mexico coastal plains: coastal herbaceous wetlands, longleaf pine/slash pine (*Pinus palustris*/*P. elliotti*) forests, shortleaf pine/oak (*P. echinata*/*Quercus* spp.) forests, loblolly pine (*P. taeda*)/hardwood forests, and bottomland hardwood forests (Newsom 1984). Coastal herbaceous wetlands range from fresh to saline waters. They frequently provide ample cover but only limited habitat because deer are restricted to higher elevations, such as natural ridges, dredge spoil deposits, and canal banks. Food abundance is adequate in freshwater herbaceous wetlands but is limited in saltwater herbaceous wetlands. Longleaf pine/slash pine habitats frequently are associated with hardwoods such as oaks. Forestry practices in this habitat type, however, frequently remove hardwood species that compete with pines - a practice that reduces carrying capacity for deer. The shortleaf pine/oak and loblolly pine/hardwood habitat types support a wide variety of plant species in the overstory and understory layers and consequently provide a relatively high carrying capacity for white-tailed deer. The bottomland hardwood habitat type provides many plant species that are food for deer. This is the most productive habitat type for deer in the coastal plains.

The Gulf of Mexico and South Atlantic coastal plains feature a mild climate (mean temperature is often from 10 to 20°C), a high precipitation rate (from 40 cm per year in south Texas to 160 cm in Louisiana), and a long growing season (from 185 to 300 days). The climate may cause greater stress to deer during the hot, humid summer than during the winter season. For example, food consumption rates of captive deer diminish during summer when ambient temperatures average 27°C and relative humidities average 75% (Short et al. 1969). Such climatic conditions may also affect the lactation capabilities of deer and the survival of fawns. The greatest environmental stress to deer in upland habitats within the coastal plains, however, may be a result of the highly leached and infertile soils, which are moderately to strongly acid and low in both organic matter and mineral nutrients. Except during spring growth, upland vegetation is usually fibrous and low in protein and minerals essential for good body growth (Short 1969; Short et al. 1969). Thus, white-tailed deer in the coastal plain have a unique problem, an abundance of forage at all seasons, but forage that is frequently nutritionally deficient during months when active plant growth is not occurring. Nutritional deficiencies exist in the availability to deer of digestible energy, digestible protein, and dietary phosphorus. The following HSI models are restricted to measures of digestible energy because more information exists about energy requirements than about nitrogen and phosphorus requirements of white-tailed deer.

Food

White-tailed deer are small ruminants that require large quantities of easily digested food in order to satisfy their metabolic requirements for maintenance, growth, and reproduction. The phenology of herbaceous and woody plant species changes throughout the year. This variation in the growth form of plants is accompanied by changes in nutrient composition and in digestibility by deer. Forages that diminish in digestibility and nutrient composition with seasons must be replaced by others of good digestibility in order to maintain deer in good health. Hence, a goal for deer managers is to provide foods that are of good digestibility and favorable nutrient composition, throughout the year.

The diet of white-tailed deer in the coastal plains is varied. During spring and early summer tender shoots, leaves and twigs of trees, shrubs and vines, and many broad-leaved herbaceous plants constitute the major portion of deer diets (Newsom 1984). Woody twigs quickly harden and lose much of their digestibility when annual growth ceases in late spring and early summer (Short et al. 1972). Grasses, after they mature in late spring and early summer, are digested so slowly as to be of little value nutritionally to deer (Short 1975). Thus, two very common forages in the coastal plain, warm season grasses and woody browse twigs, are of little nutritional importance to white-tailed deer by early summer and thereafter. A variety of other food is important during the remainder of the year. Seeds and fruits, especially acorns, represent palatable and highly digestible foodstuffs from summer into winter (Short and Epps 1976). Cool season herbages that grow during winter and early spring are highly digestible foodstuffs until these forages mature during late spring (Short and Segelquist 1975). Deciduous leaves of woody browse plants retain high digestibility until leaf fall, and evergreen leaves of woody browse plants retain their nutritional value throughout the year (Short et al. 1975). Edible fungi may be similarly useful throughout the year.

The HSI models described in this paper emphasize the measurement of food items such as cool season herbages, leaves of woody browse plants, edible fungi, and various seeds and fruits as important components in the evaluation of the quality of habitat for white-tailed deer during autumn-winter.

Water

Readily available sources of fresh water are important components of white-tailed deer habitat in the coastal plain (Newsom 1984). The extent and frequency of water consumption by deer depend on the ambient temperature, the animal's physical condition, and the kinds of foods consumed (Marchinton and Hirth 1984). Deer may be able to survive without surface water for some period of time if rainfall, humidity, and plant succulence are relatively high.

The HSI models assume that available water for drinking is required by white-tailed deer and arbitrarily assume that available water must be present within 1.6 km of the site being evaluated for that location to be considered potential habitat for white-tailed deer.

Cover

Cover provides more of a refuge for deer from man and dogs than from harsh winter weather in the coastal plains. Harlow (1984) lists swamps and dense honeysuckle (*Lonicera* spp.)-thicketed areas as suitable cover but otherwise offers no definition of what constitutes adequate deer cover or shelter. I suggest that cover adequate for deer might consist of an 8-ha area (within each 40 ha of habitat) where cover is sufficiently dense, that a 1.5-m white pole is not visible at a distance ≥50 m.

Cover is usually adequate for white-tailed deer in coastal habitats, except perhaps in large tracts of recently cleared forest lands, or in areas where brush has been cleared to favor grass production (Halls 1978).

Reproduction

The reproductive physiology of white-tailed deer is reviewed by Verme and Ullrey (1984). These physiological processes probably apply equally well to the different populations of deer that exist within the geographical area of the coastal plains. Deer from upland sites within the coastal plains are frequently of small size. This may be due to upland sites usually having highly leached and infertile soils, which are moderately to strongly acid and low in both organic matter and mineral content. Except during spring growth the vegetation on these upland sites is frequently fibrous and low in protein and minerals essential for good body growth. Dietary deficiencies in upland sites probably limit deer numbers as well as their size. Substantial fawn losses may occur when deer consume nutritionally deficient diets. High ambient temperatures can also directly affect the lactation of does, and growth rate and survival of fawns (Short et al. 1969). These suggested impacts are not well substantiated in the literature. They are mentioned here to emphasize that the nutritional considerations mentioned in the present models should also be expected to influence the reproductive capabilities of white-tailed deer on the coastal plains.

Interspersion

White-tailed deer require suitable food, cover, and water. Probably the ideal mix of these three components in the coastal plains would be blocks of dense cover within forested areas having limited tree canopy cover (to insure understory food production) and common sources of fresh water. This ideal structure for deer habitats probably rarely occurs in nature, where forest succession usually leads to a dense tree canopy with limited understory food reserves. Nor does it occur where intensive forest management or agricultural management practices, such as the clear-cutting of pine timber, regeneration of forest stands by planting young pines, thinning of young pine stands, and removal of competing hardwoods, are prevalent. Early regenerative forest stages provide abundant forages for deer, and the periodic thinning of established plantations may provide some additional food. These silvicultural practices need to be coordinated over area and time to provide suitable foods for deer throughout the lifetime of a forest stand.

The establishment of food plots may be a good compromise between silvicultural practices and deer requirements within the coastal plains. Food plots, if intensively managed to produce cool season herbages, woody plants with evergreen leaves, and fruits and seeds, provide a habitat condition that varies only nominally from the ideal habitat structure described above. The tree canopy is allowed to close over much of the forest but is kept open over food plots, which should be abundant (accounting for 2% or more of the total land area), well distributed, and relatively small (0.4-0.8 ha) (Crawford 1984).

The existence of deer in habitats that are broken mixes of forests and agricultural lands reflects the great adaptability and tolerance of white-tailed deer, rather than favorable interspersion patterns of habitats. These habitat mixes vary substantially from the proposed ideal habitat structure described above. I do not try to represent the variations in the structure of habitats from the proposed ideal structure of habitats with any particular variable in the following HSI models. I do describe an extreme condition wherein large blocks of habitat with inadequate cover (measured in terms of area) are considered to provide an inadequate structure and to be inadequate habitats for deer.

HABITAT SUITABILITY INDEX (HSI) MODELS

Model Applicability

Geographic area. The models for the white-tailed deer described here were developed for the South Atlantic and Gulf of Mexico coastal plains (Figure 1). The models are restricted to this range because they are based on results of controlled feeding studies with captive deer conducted at Louisiana State University, Baton Rouge (Fowler et al. 1968; Short et al. 1969), and on results from an extensive series of experiments that described the phenology, composition, and digestibility of forages in the gulf coastal plain.

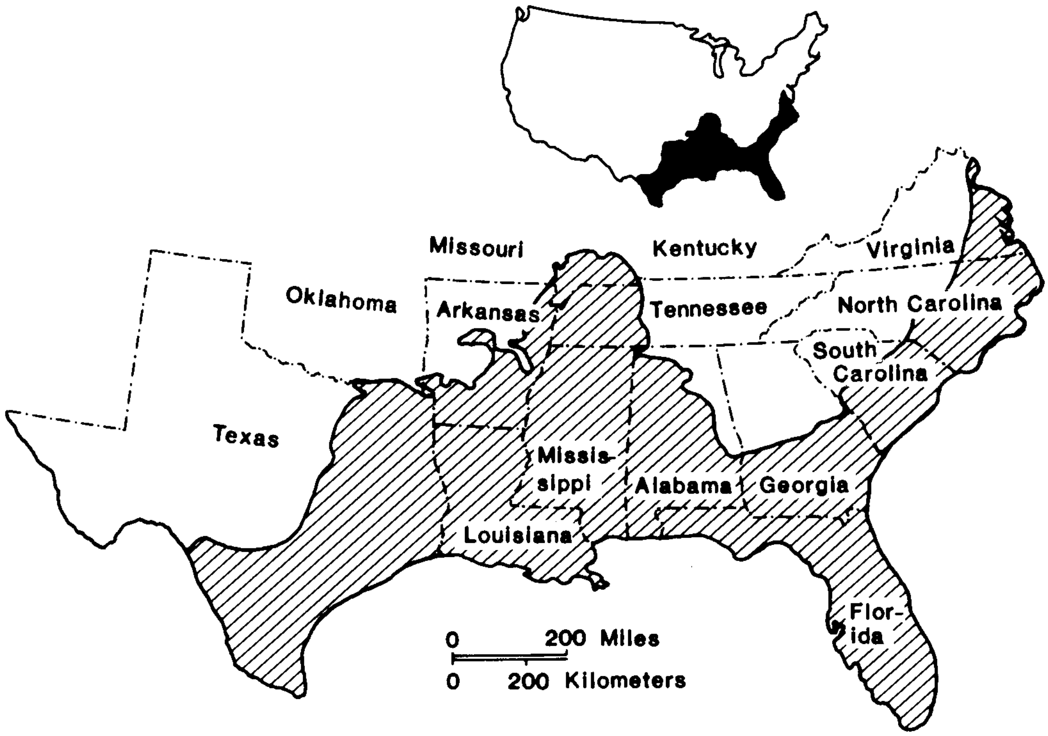

Figure 1. These models for the white-tailed deer are considered most applicable for the area of the South Atlantic/Gulf of Mexico coast delineated on the above map (after Newsom 1984:368).

Season. The models provide an estimate of the quality of habitat for the white-tailed deer during autumn-winter. This is a stress period for deer, not because of the severity of the southern winter, but because of the limited quality of many forages during these months.

Cover types. The models were developed for application in habitats described as Forests, Tree Savanna, Forested Wetland, Shrubland, Shrub Savanna, Scrub-Shrub Wetland, Grassland, Pasture and Hayland, Forbland, Herbaceous Wetland, and Cropland (U.S. Fish and Wildlife Service 1981).

Minimum habitat area. The minimum habitat area is defined as the minimum amount of contiguous habitat that is required before a species will live and reproduce in an area. Average home-range sizes for nonmigratory white-tailed deer on the coastal plains, summarized from several studies, varied from 59-520 ha (Marchinton and Hirth 1984). I suggest in these models that land units should be ≥40 ha (0.4 km^2) in area before they are evaluated as habitats for deer.

Verification level. The models were developed from quantitative information about body weight, rates of food intake of captive deer during the autumn-winter, and estimated digestibility values for a variety of forages growing in southern forests. The models also rely on a variety of published information about the metabolic requirements of mammals, the physiological attributes of ruminants, and the energy values of different plant parts. The HSI values from these models describe the potential of a habitat to supply food energy to white-tailed deer. The models are designed to rank the suitability of various southern habitats as would a biologist with expert knowledge about the habitat requirements of deer. The models should not be expected to rank habitats in the same way that population data would, because many nonhabitat-related criteria can significantly impact populations of wildlife species.

Model Descriptions

Overview. Four related HSI models are described below. Model I is the most complex and estimates the carrying capacity of habitats during autumn-winter on the basis of the energy requirements of deer during these seasons. Model II is of lower resolution. It is derived from Model I and is also driven by intensive field sampling to determine quantities of suitable forage on an evaluation area. Model III (also derived from Model I), provides a more general estimate of habitat quality because only very general estimates of forage abundance are utilized. Model IV is of even lower resolution and only predicts the probable presence or absence of deer on an evaluation area.

Each of these models is driven by estimates of the quantity of suitable forage on a study area. The selection of the appropriate model for a study effort is determined by the type of information required, which, in turn, dictates the level of field effort that must be expended. The following examples illustrate how the appropriate model might be selected.

An explicit statement is required about the probable quality of a habitat for white-tailed deer during autumn-winter.	Models I and II
A general statement is required about the probable value of a habitat for white-tailed deer during autumn-winter.	Model III
A general statement is required about the probable presence or absence of white-tailed deer on a habitat during autumn-winter.	Model IV

The four models vary in resolution because they are driven by estimates of forage abundance that vary from highly quantified to descriptive. Sections within the models document the logic and the assumptions used to translate habitat information for white-tailed deer into the variables selected for the models. These sections also describe the assumptions inherent in the models, identify the variables used in the models, define and justify the suitability levels of each variable, and describe the assumed relationships between variables.

Habitat layers. A variety of forest products important to deer occur in the different habitat layers of a forest community (Figure 2). The white-tailed deer, in the guilding context of Short (1983), can be considered to forage in the understory and midstory layers and to breed in the understory layer. Other layers of habitat, however, contribute products useful to deer.

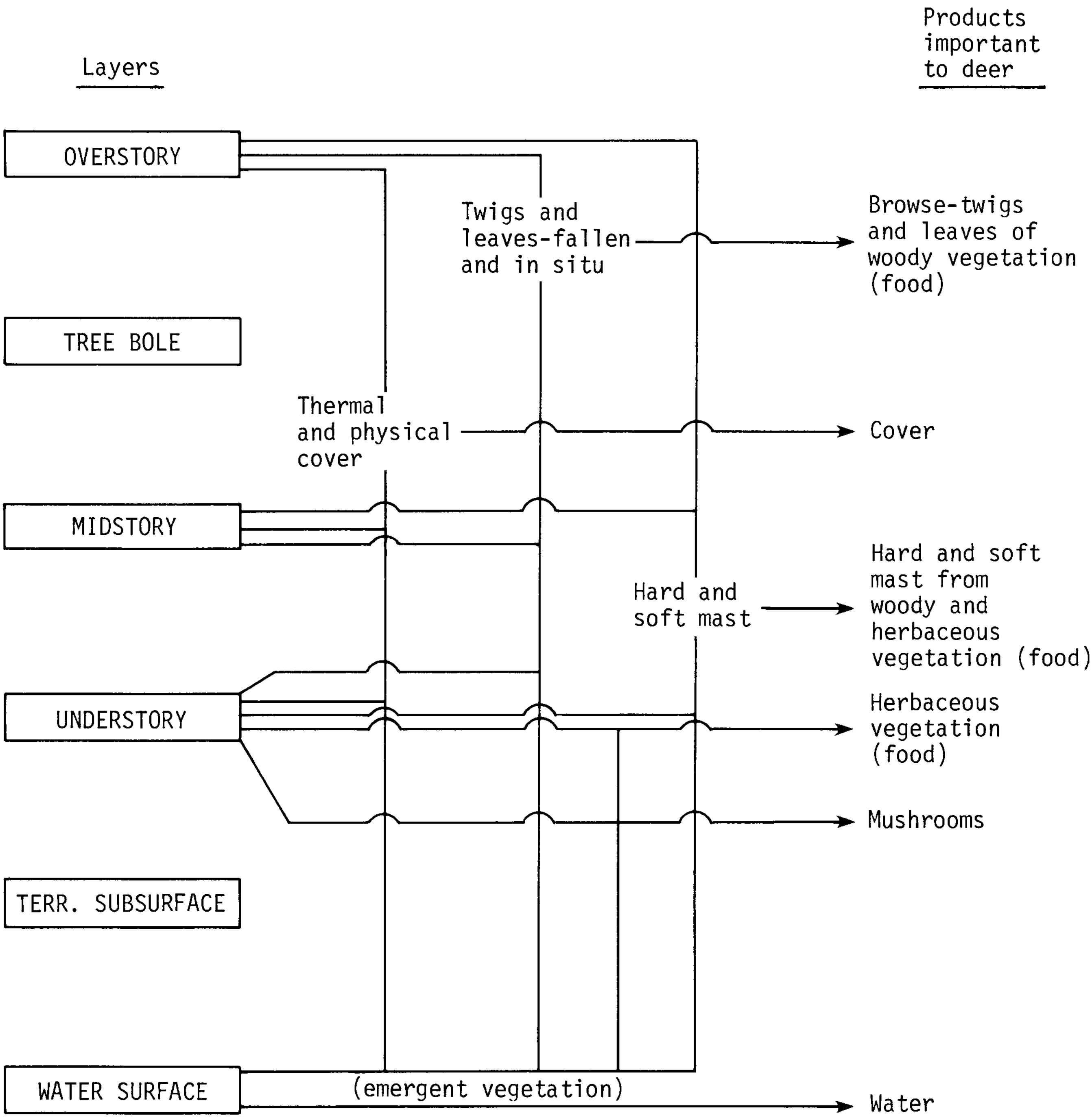

Figure 2. The products from different layers of habitat that contribute to the quality of habitat for white-tailed deer.

The requirements for physical and thermal cover, for example, can be provided by the overstory canopy, by the midstory canopy, by emergent herbaceous and woody vegetation in the surface water layer of temporary wetlands, and by topographic features and/or woody and herbaceous vegetation in the understory layer.

Forage items include leaves and twigs dislodged from woody stems in the overstory and midstory layers and leaves and stems *in situ* in the midstory, in the understory, and on emergent vegetation in the water surface layer of temporary wetlands. Preferred dietary items also include a variety of hard and soft mast dislodged from the overstory and midstory layers and hard and soft mast *in situ* in the midstory, understory, and in suitable emergent vegetation in the water surface layer of temporary wetlands. Food components also include broad- and narrow-leaved herbaceous components from the understory and from the water surface layer of temporary wetlands, and fungi from the understory layer. Free water for drinking is assumed to be a necessity in these models.

Metabolic requirements of deer. It is necessary to estimate the metabolic requirements of deer to estimate the carrying capacity of habitats in these models. The metabolic requirements of deer in the gulf and South Atlantic coastal plains have not been measured. A surrogate measure is the interspecies mean basal metabolic rate (BMR) multiplied by some value that indicates that usual physical activity requires energy in excess of basal rates. The interspecies mean metabolic rate is estimated by expanding measured or estimated body weight (kg) to the 0.75 power ($kg^{0.75}$) and multiplying by 70 to calculate requirements in kcal per day. Wallmo et al. (1975) estimated the activity metabolic rate (AMR), which represents normal physical activity of Colorado mule deer (*Odocoileus hemionus*) in winter, to be about 2.0 times the basal metabolic rate. They also estimated that the activity metabolic rate might be about 2.3 times the basal metabolic rate for lactating females and about 2.5 times the basal metabolic rate for males during the rut. Mautz (1978) presented a calculation of carrying capacity based on an energy expenditure rate of 150 $kcal/kg^{0.75}/day$ - a value equal to about 2.1 times the basal metabolic rate. Moen (1973) lists data estimating the energy expenditure of a deer in autumn that was bedded 18% of the time, standing 18% of the time, and walking 64% of the time as 1.67 times the basal metabolic rate, and an energy expenditure during winter when the deer was bedded 25% of the time, standing 25% of the time, and walking 50% of the time as 1.59 times the basal metabolic rate. I have assumed from these estimates and measurements that a factor of 1.8 times the basal metabolic rate might be a reasonable approximation of the activity metabolic rate of does, for purposes of this model. I have assumed, for reasons described below, that the activity metabolic rate of male deer during the November-December rut is 2.1 times the basal metabolic rate.

The body weights and rates of food consumption listed in Table 1 for southern deer were determined for captive deer fed a nutritionally adequate ration *ad libitum* under controlled conditions (Fowler et al. 1968; Short 1969). The estimated energy requirements (kcal/day) of these deer also varied during autumn-winter. An average energy requirement of 2,845 kcal/day for bucks and of 2,098 kcal/day for does was calculated from these data. I selected these values to represent the average energy requirements of male and

Table 1. Measured body weights and food consumption rates (after Fowler et al. 1968) and estimated energy requirements (kcal/day) for male and female white-tailed deer during autumn-winter in the coastal plains. The probable gross energy value of wild foodstuffs during each month is also listed.

Sex	Month	Age[a] (months)	Body wt. (kg)	Food intake rate (g/kg/day)	Metabolic body wt. ($kg^{0.75}$)	Activity metabolic rate	Estimated energy requirement (kcal/day)	Gross energy value of wild foodstuffs (kcal/g)
Male	Oct.	16	64	22	22.6	1.8	2848	4.3
	Nov.	17	63	15	22.4	2.1	3293	4.8
	Dec.	18	60	17	21.6	2.1	3175	4.8
	Jan.	19	56	20	20.5	1.8	2583	4.3
	Feb.	20	57	20	20.7	1.8	2608	4.3
	Mar.	21	58	21	21.0	1.8	2646	4.3
	Apr.	22	62	24	22.1	1.8	2785	4.3
Mean			60.4	20.5	21.7	1.9	2845	
Female	Sept.	15	40	28	15.9	1.8	2003	4.3
	Oct.	16	42	27	16.5	1.8	2079	4.3
	Nov.	17	44	22	17.1	1.8	2155	4.8
	Dec.	18	43	20	16.8	1.8	2117	4.8
	Jan.	19	43	17	16.8	1.8	2117	4.3
	Feb.	20	42	19	16.5	1.8	2079	4.3
	Mar.	21	42	18	16.5	1.8	2079	4.3
	Apr.	22	44	22	17.1	1.8	2155	4.3
Mean			42.5	21.6	16.6	1.8	2098	

[a] Assumes a June 15 birth date.

female deer during the autumn-winter season. These values will obviously be in error if the body weights listed in Table 1 do not reflect the body weights of wild deer, or if the true activity metabolic rates of wild deer differ significantly from the assumed rates. Actual weights of deer from coastal plains habitats could be used to refine the estimated metabolic requirements. Male and female deer differ in their metabolic requirements. I have used the average metabolic requirements of a deer unit consisting of two does and one buck to simplify the HSI calculation. This weighted average of the energy requirement for a deer unit during autumn-winter in the coastal plains is about 2,400 kcal/day.

Model I. The HSI model based on energy concepts. This model is similar in concept to models described by Moen (1973), Wallmo et al. (1977), and Mautz (1978). Habitat carrying capacity in Model I is estimated for the autumn-winter period (November 15 - February 15), when quality foods available to deer in the coastal plain are less common than at other seasons. The energetics model is quite general to help reduce the amount of field data required for implementation. Still, intensive sampling is required to use the model. The energetics model provides both a rationale for developing models II-IV and a way to assess how those models mimic results from the energetics model. The logic for the energetics model is shown in Figure 3. I assume in this model that free water is required by deer within their normal home range, although Marchinton and Hirth (1984) suggest that white-tailed deer can survive without free water when rainfall, humidity, and plant succulence are relatively high. Free water is assumed to be required within 1.6 km of the habitat block being evaluated, because the home range of white-tailed deer usually does not exceed 2.6 km^2 [observations of Severinghaus and Cheatum (1956) cited in Marchinton and Hirth (1984)].

Habitats to be evaluated for white-tailed deer in the southern forest type should be relatively large blocks of land that provide thermal and/or protective cover to deer. Habitat blocks should be at least 40 ha (0.4 km^2) in area and provide suitable cover on at least 20% of the area. Cover may be provided by overstory-midstory layer canopies, by dense (undefined) vegetation in the understory layer, by dense (undefined) vegetation (e.g., cattails, *Typha* spp.) in temporary herbaceous wetlands, or by suitable topographic features.

The determination of an HSI value for this model involves estimating the amount of energy metabolically available to deer on a study area and comparing that estimate to the amount of metabolizable energy (ME) available to deer on a standard unit of habitat. The HSI determination is actually an estimate of the relative carrying capacity of the study area. The numerator of the HSI calculation is the sum of the product of the quantity of each forage class present on a hectare of habitat (QF), times the digestibility of each forage class (DF), times values (EV) that will express the product of QF and DF in terms of metabolizable energy (ME). This numerator is compared to a denominator that represents the metabolizable energy available in a "standard" habitat unit. I arbitrarily designated that "standard" habitat unit to be a hectare of habitat that will provide 100,000 kcal of metabolizable energy for deer. Habitats that provide fractions of that 100,000 kcal of metabolizable energy receive fractional HSI values. Habitats that provide more than 100,000 kcal

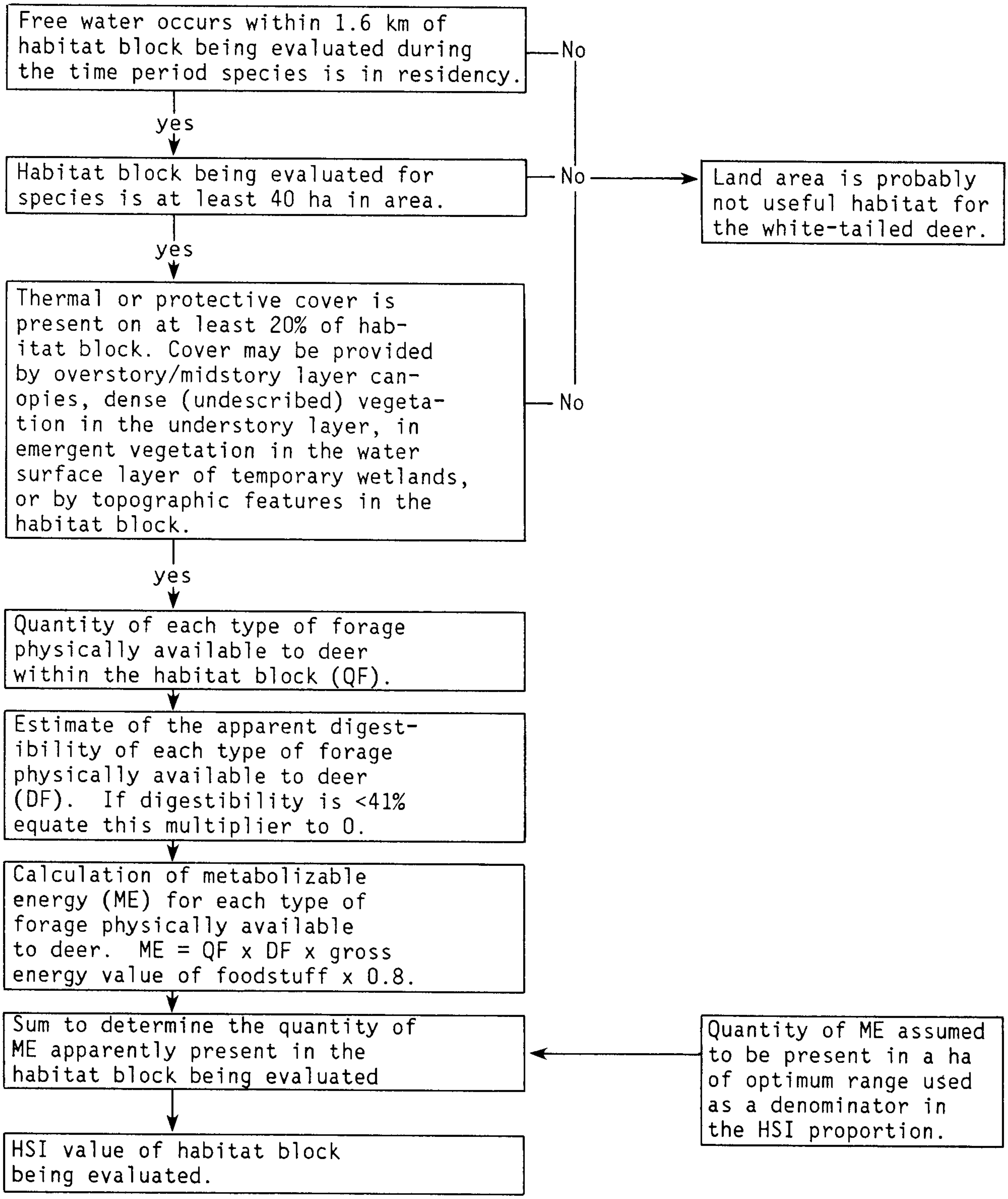

Figure 3. Logic used to develop the energetics model (Model I) to provide an HSI determination of habitat quality for the white-tailed deer.

of metabolizable energy receive HSI values rounded to 1.0. For purposes of discussion, a hectare of habitat that provides 45.5 kg of food that is 64% digestible and contains 4.3 kcal/g provides 100,000 kcal ME/ha. Such a "standard" habitat unit could provide about 41-42 deer-days use for a deer unit (2,400 kcal/day). The "standard" habitat unit could provide metabolizable energy during the autumn-winter season equivalent to that required for 46 deer for a 90-day autumn-winter season (November 15 to February 15) per square kilometer of habitat - a high deer density. The desired carrying capacity is, of course, some fraction of this maximum value so that suitable foodstuffs will not be overutilized, which might limit their availability in subsequent years.

The Habitat Suitability Index (HSI) for the energetics model (Model I) has the following general format:

$$HSI = \frac{\text{carrying capacity of the habitat being evaluated}}{\text{carrying capacity of a unit of "standard" habitat}} \qquad (1)$$

The actual equation for calculating HSI is as follows:

$$HSI = \frac{\sum_{i=1}^{n} (QF_i \times DF_i \times EV_i)}{100{,}000 \text{ kcal ME/ha}}$$

where $i = 1, \ldots, n$ = The classes of suitable forages existing in measureable quantities on a hectare of habitat.

QF_i = The quantity (grams) of individual classes of suitable forage available within 1.5 m of the ground on each hectare of habitat to be evaluated (a suitable forage for deer in the gulf and South Atlantic coastal plains is a type of vegetation whose digestibility in autumn-winter is estimated or determined to be ≥41%).

DF_i = The apparent digestibility of each class of suitable forage. A digestibility of a forage for deer during the autumn-winter in the gulf and South Atlantic coastal plains <41% is considered to be a digestibility of 0.

EV_i = The energy value of each forage class is equal to the apparent gross energy (GE) value of each class of suitable forage times the constant 0.8, which will provide an estimate of metabolizable energy (ME) after forage digestible energy (DE) values have been determined.

100,000 kcal ME/ha = the amount of metabolizable energy (ME) available to deer on a unit of standard habitat

The HSI equation is general and may have relevance throughout the range of white-tailed deer. The values for DF and EV have been determined from empirical studies in the gulf and South Atlantic coastal plains. The HSI equation may have applicability to other deer ranges in North America if specific values for forage digestibility and the energy value of each forage class can be established. The value for quantity of suitable forage needs to be determined for each range under study.

Estimating quantity of forage (QF). The quantity of forage (g dry matter/ha) in the energetics model requires the determination of the quantity of different types of vegetative food available within 1.5 m of the ground in the habitat blocks to be evaluated. Classes of vegetation are quantified separately because they vary in abundance, phenology, composition, digestibility, and preference to deer. Quantities of the following seven forage classes are candidate forage types to be evaluated in the coastal plains. Forage classes 3 to 7, below, are emphasized in these models because, as indicated below, they provide sufficient digestible energy to deer in the Gulf of Mexico and South Atlantic coastal plains to maintain deer with only minimum weight losses during autumn-winter.

1. current year's twig growth and needles from pines

2. leaves of current year fallen from perennial woody species

3. leafy browse composed of evergreen or tardily deciduous leaves *in situ* on perennial woody species

4. mast from all layers including acorns, fleshy fruits, and seeds from many agricultural crops

5. leguminous seeds

6. cool season grasses and forbs including growing herbaceous agricultural crops

7. mushrooms

Other foods, such as mature and hardened warm-season grasses, mature and hardened warm-season forbs, mature and hardened woody twigs, and dried fruits are common forages whose relative abundance need not be considered in this evaluation model because they are of limited digestibility to deer.

Estimating digestibility of forage (DF). Forages differ in digestibility because their nutrient composition is different. Several studies of forages grown in the coastal plains have described how southern forages differ in apparent digestibility (Short et al. 1975; Short and Epps 1976; Blair et al. 1977). Estimates of dry matter digestibility cited below were determined using the nylon bag technique, wherein small quantities of individual foodstuffs were inserted into the rumen of cannulated goats used as domestic animal analogues for deer. The forage digestibility estimates have not been correlated with true digestibility coefficients, although they have been compared with estimates of digestibility calculated with the summative equation (r^2 = 0.62, Short et al. 1974), and forage digestibility values determined with the summative equation have been compared with true digestibility coefficients.

All vegetation has a nutrient and caloric content, but not all vegetation should be considered suitable food for southern deer. This is illustrated in Tables 2 and 3. These tables contain estimates of the forage digestion rates required so that deer may survive the autumn-winter period with either minimum or maximum allowable weight losses. The calculations are based on the energy requirements of deer at different estimated activity metabolic rates, the contribution to energy requirements supplied by metabolizable energy, the rate of forage intake estimated from feeding trials with captive deer, the estimated caloric value of individual foodstuffs, and the constant (0.8), which estimates metabolizable energy (ME) from apparent digestible energy (DE). The values in Tables 2 and 3 indicate that deer must eat more digestible forages to maintain the same condition if activity metabolic rates increase, and that bucks may have an increased activity metabolic rate while in rut during November and December, if bucks and does digest the same foodstuffs equally well. The forage classes that may provide the required levels of metabolizable energy to deer are also listed in Tables 2 and 3. I suggested earlier that an activity metabolic rate of 1.8 might be a suitable multiplier of the basal metabolic rate for female deer during autumn-winter. Female deer may require forages that are 64% digestible to achieve minimum weight loss during autumn-winter and they may require forages that are ≥41% digestible during autumn-winter to sustain life with the maximum survivable weight loss (Table 2). Male deer may also require forages that are 64% digestible to achieve minimum weight loss, but may require forages that are ≥46% digestible during autumn-winter to sustain life with the maximum survivable weight loss (Table 3). Very common forages, such as mature and hardened warm-season grasses (digestible dry matter (DDM) = 20%), mature and hardened warm-season forbs (DDM = 27%), and terminal segments of mature and hardened woody twigs (DDM = 28-40%), are apparently not suitable food for southern deer during autumn-winter. These forages will not yield sufficient metabolizable energy to maintain deer within the arbitrary limits of a maximum 30% weight loss. Note that these very common forages were not included in the lists of classes of forages to be sampled on evaluation plots. If the correct activity metabolic rate was actually lower than my estimate of 1.8 then forages with reduced digestibility could be used by deer during autumn-winter to sustain life. For example, if the activity metabolic rate during autumn-winter was actually 1.6 then does could use forages with digestibilities as low as 33% (Table 2), so that forages like dried fruits and the terminal portions of woody twig tips could also provide necessary metabolizable energy during autumn-winter. The listing for forage digestibility (DF) provides an estimate of dry matter digestibility in major forage classes available during autumn-winter in the coastal plains. I

Table 2. Required rates of forage digestion to provide energy for female deer at a minimum (4.5% weight loss observed for *ad libitum* fed deer in confinement, raw data in Table 1) and maximum survivable weight loss (assumes 30% weight loss over a 90-day autumn-winter period) at different activity metabolic rates.

Activity metabolic rate	Required forage digestion rate for minimum autumn-winter weight loss#	Forages providing the necessary metabolizable energy*	Required forage digestion rate for maximum survivable autumn-winter weight loss#	Forages providing the necessary metabolizable energy*
1.5	53	h,i,j,k,l	29	d,e,f,g,h,i,j,k,l
1.6	57	h,i,j,k,l	33	d,e,f,g,h,i,j,k,l
1.7	60	h,i,j,k,l	37	d,e,f,g,h,i,j,k,l
1.8	64	h,i,j,k,l	41	f,g,h,i,j,k,l
1.9	68	i,j,k,l	45	g,h,i,j,k,l

#Calculated as: required rate of forage digestion for female deer = 43 $kg^{0.75}$ (average metabolic body weight November to December, see Table 1) × 70 (interspecies mean metabolic rate) × activity metabolic rate (varies in example) - metabolizable energy contribution (133 kcal/day under conditions of minimum weight loss; 860 kcal/day under conditions of maximum survivable weight loss) ÷ 19.5 g/kg (average food consumption rate November to February; see Table 1) × 43 kg (average body weight November to February; see Table 1) × 4.6 kcal/g (assumed energy value of mixed diet of 67% roughages, 33% seeds) × 0.8 (conversion factor of digestible energy to metabolizable energy).

*Estimated rates of forage digestion of foodstuffs during autumn-winter (from Short et al. 1975; Short and Epps 1976; Blair et al. 1977).

a = 20% (mature and hardened warm-season grasses; this common forage does not provide sufficient energy for any of the activity metabolic rate scenarios)

b = 27% (mature and hardened warm-season forbs)

c = 28% (mature and hardened woody twigs, terminal 10 cm)

d = 39% (dried fruits: samaras, achenes, carpels, nutlets)

e = 40% (terminal 5 cm portions of twigs with terminal buds from perennial woody species)

f = 44% (current year's twig growth and needles from pines)

g = 45% (leaves of current year fallen from perennial woody stems)

h = 65% (leafy browse composed of evergreen or tardily deciduous leaves *in situ* on perennial woody stems)

i = 68% (mast from all layers including acorns, fleshy fruits, and seeds from many agricultural crops)

j = 87% (leguminous seeds)

k = 94% (cool-season grasses and forbs including growing herbaceous agricultural crops)

l = 95% (mushrooms)

Table 3. Required rate of forage digestion to provide energy for male deer at a minimum (12.5% weight loss observed for *ad libitum* fed deer in confinement, raw data in Table 1) and maximum survivable weight loss (assumes 30% weight loss over a 90-day autumn-winter period) at different activity metabolic rates.

Activity metabolic rate	Required forage digestion rate for minimum autumn-winter weight loss#	Forages providing the necessary metabolizable energy*	Required forage digestion rate for maximum survivable autumn-winter weight loss#	Forages providing the necessary metabolizable energy*
1.5	42	f,g,h,i,j,k,l	24	b,c,d,e,f,g,h,i,j,k,l
1.6	46	h,i,j,k,l	28	c,d,e,f,g,h,i,j,k,l
1.7	50	h,i,j,k,l	32	d,e,f,g,h,i,j,k,l
1.8	53	h,i,j,k,l	35	d,e,f,g,h,i,j,k,l
1.9	57	h,i,j,k,l	39	d,e,f,g,h,i,j,k,l
2.0	61	h,i,j,k,l	43	f,g,h,i,j,k,l
2.1	64	h,i,j,k,l	46	h,i,j,k,l

#Calculated as: Required rate of forage digestion for male deer = 60.8 $kg^{0.75}$ (average metabolic body weight October-January; see Table 1) × 70 (interspecies mean metabolic rate) × activity metabolic rate (varies in example) - catabolizable energy contribution (533 kcal/day under conditions of minimum weight loss; 1280 kcl/day under conditions of maximum survivable weight loss) ÷ 18.5 g/kg (average food consumption rate November-February; see Table 1) × 4.6 kcal/g (assumed energy value of mixed diet of 67% roughages, 33% seeds) × 0.8 (conversion factor of digestible energy to metabolizable energy).

*Forages identified in Table 2.

have assumed that the quantity of forages (QF) can be determined from field sampling efforts and that the estimate of the true digestibility of those forage classes can be approximated from the following listing.

1.	current year's twig growth and needles from pines	= 44% DDM
2.	leaves of current year, fallen from perennial woody stems	= 45% DDM
3.	leafy browse composed of evergreen or tardily deciduous leaves _in situ_ on perennial woody stems	= 65% DDM
4.	mast from all layers including acorns, fleshy fruits, and seeds from many agricultural crops	= 68% DDM
5.	leguminous seeds	= 87% DDM
6.	cool season grasses and forbs including growing herbaceous agricultural crops	= 94% DDM
7.	mushrooms	= 95% DDM

Estimating energy values of forage. The energy values (EV) of forage are dependent on the presumed caloric value of each class of forage. Few determinations of the caloric values of southern forages have been made. Blair et al. (1977) list the caloric values for composite samples of grasses, forbs, browse leaves and twig tips, browse twigs, pine needles and twigs, mushrooms, and fruits at the four seasons to be about 4.35 kcal/g dry matter. Golley (1961) determined that many forages containing carbohydrates have a similar gross energy (GE) value of 4.3 kcal/g dry matter. Seeds, because of their high lipid content, have a gross energy value of about 5.1 kcal/g dry matter. The gross energy value of most forages consumed during autumn-winter is assumed, for this model, to be about 4.3 kcal/g dry matter. The gross energy value of seeds such as acorns is assumed to be about 5.1 kcal/g dry matter.

The gross energy value of a forage is a laboratory measure. This gross energy value is never realized by deer because dry matter digestion is usually not complete and there is work associated with the digestion of roughages. Digestible energy is calculated as the gross energy value of a forage minus the gross energy value of the feces produced from eating that forage. The calculation of metabolizable energy also recognizes that energy associated with urine and eructated gases of fermentation are costs of digestion that further diminish the quantity of energy available to deer from a food. Moen (1973) suggested that the metabolizable energy of forages for deer can be estimated as 80% of the digestible energy of that food. This value (0.8) is used as a constant multiplier in this model. The energy value (EV) thus assigns a caloric value to a class of forage and transforms that caloric value to a measure, which when multiplied by forage digestibility values, provides estimates of metabolizable energy.

EV of most roughages = 4.3 kcal/g x 0.8
EV of most seeds = 5.1 kcal/g x 0.8

Model II. Representing the energetics model with Suitability Index (SI) curves. The energetics model can be expressed in the more usual HSI format. The quantity (QF), digestibility (DF), and energy values (EV) of forages are condensed into two variables (quantity and digestibility of forage) in Model II. The calibration of the two variables is directly dependent on calculations developed and assumptions made for the energetics model. The logic used in this second HSI model is shown in Figure 4. The same restrictions about block size and water and cover availability in habitats apply for Model II as applied for Model I. Model II, as was true for the energetics model, is intended to evaluate the relative quality of habitats during autumn-winter for white-tailed deer in the Gulf of Mexico and South Atlantic coastal plains.

The quantity of forage in forage classes 1-7, identified in Model I, can be assigned an SI value by consulting Figure 5. The discussion for Model I suggested that habitats that provided 100,000 kcal of metabolizable energy/hectare should receive an HSI of 1.0. This value would be realized if a habitat provided ≥45.5 kg of forage dry matter that was ≥64% digestible. An SI value of 0.0 is assigned to forage quantity (QF) if no suitable forage is present, and an SI of 1.0 is assigned to forage quantity (QF) if ≥45.5 kg dry matter of suitable forage is present (Figure 5).

The digestibility of forages in forage classes 1-7, identified in Model I, can be assigned an SI value by consulting Figure 6. The discussion for Model I suggested that forages with an apparent digestibility <41% might not provide sufficient metabolizable energy to maintain deer during the autumn-winter stress period. Forages that are <41% digestible are thus assumed to have an SI value of 0.0 in this model. The data in Tables 2 and 3 also suggest that forages ≥64% in digestibility produce sufficient metabolizable energy to maintain deer with only minimum weight losses during autumn-winter. Digestibility values ≥64% are thus assumed to have an SI value of 1.0 in this model.

HSI determination. The Habitat Suitability Index (HSI) for evaluating the quality of southern forest habitats for white-tailed deer is determined from the summed product of SI values representing the quantity and digestibility of each forage class present in a study area. The conceptual

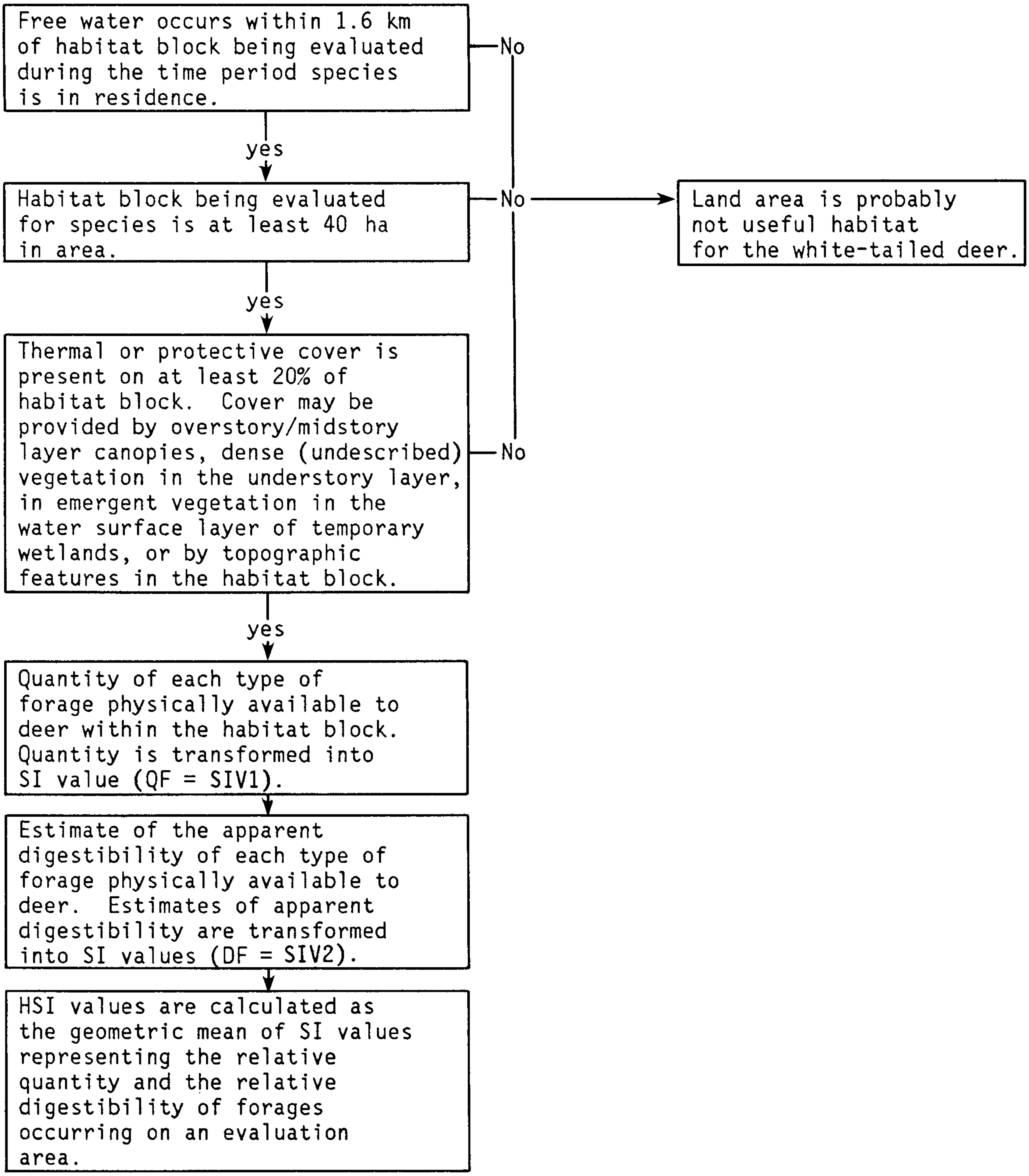

Figure 4. Logic used to develop HSI Model II for white-tailed deer based on SI curves representing the quantity of forage on an evaluation area and the apparent digestibility of those forages.

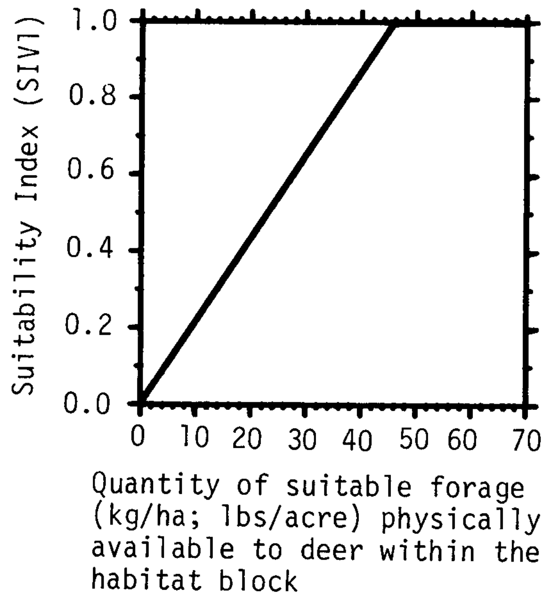

Figure 5. SI values for QF increase as the quantity of suitable forage increases per ha of habitat.

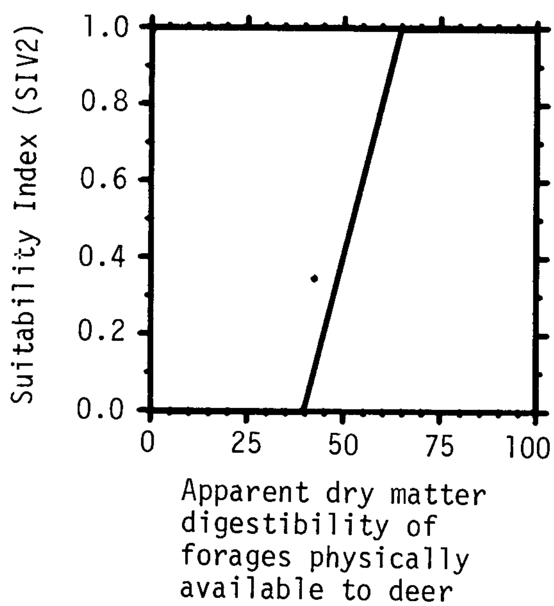

Figure 6. SI values increase as the apparent digestibility of forage increases from 41% to 64%.

approach is comparable to the logic developed in the energetics model. The equation for estimating the suitability of habitats for white-tailed deer is given below. HSI's greater than 1.0 are rounded to 1.0.

$$HSI = \sum_{i=1}^{n} (SIV1_i \times SIV2_i)^{1/2} \qquad (2)$$

where $i=1, \ldots, n$ = The classes of suitable forages existing in measurable quantities on a ha of habitat.

$SIV1_i$ = the quantity (QF) of each type of suitable forage (a suitable forage is a type of vegetation whose digestibility by deer is estimated or determined to be ≥41%) on each ha of habitat to be evaluated as represented by the appropriate SI value.

$SIV2_i$ = the apparent digestibility (DF) of each class of suitable forage as represented by the appropriate SI value.

Model III. The relative abundance of foods in a habitat block. Model III is applicable when only general information about forage abundance is available from a habitat block. Resolution is fairly low with this model and only general statements of habitat quality are possible. The logic used in developing this model is shown in Figure 7. The same restrictions about block size and water and cover availability in habitats apply for Model III as applied for Model I.

Models I and II, as described above, are driven by measures of the abundance of different types of deer foods within an evaluation area. Quantitative measures of food abundance include clip-weigh techniques for estimating quantities of grass, forb, and browse tissues; establishing, maintaining, and monitoring seed traps to measure weights of fruits and seeds; and periodic sampling along transects to measure mushroom production.

Surrogate variables that are quick and easy to measure are sometimes used when it is not feasible to measure food production directly or intensively. It is assumed that the surrogate variables approximate food abundance and that an HSI developed from them approximates habitat quality. These are frequently untested assumptions. Surrogate variables may be visual estimates along transects or subplots. Visually estimating the weight of current annual growth is rapid, and a large number of plots can be examined in a relatively short time. With training, most observers can estimate within 10 to 15% of the actual value. The big disadvantage is that the estimates are subjective, their relation to actual values is not known, and the results are apt to be biased (Wenger 1984:711). The count of mast-bearing plants per hectare or of the basal area of mast trees is a surrogate measure of the production of shrub

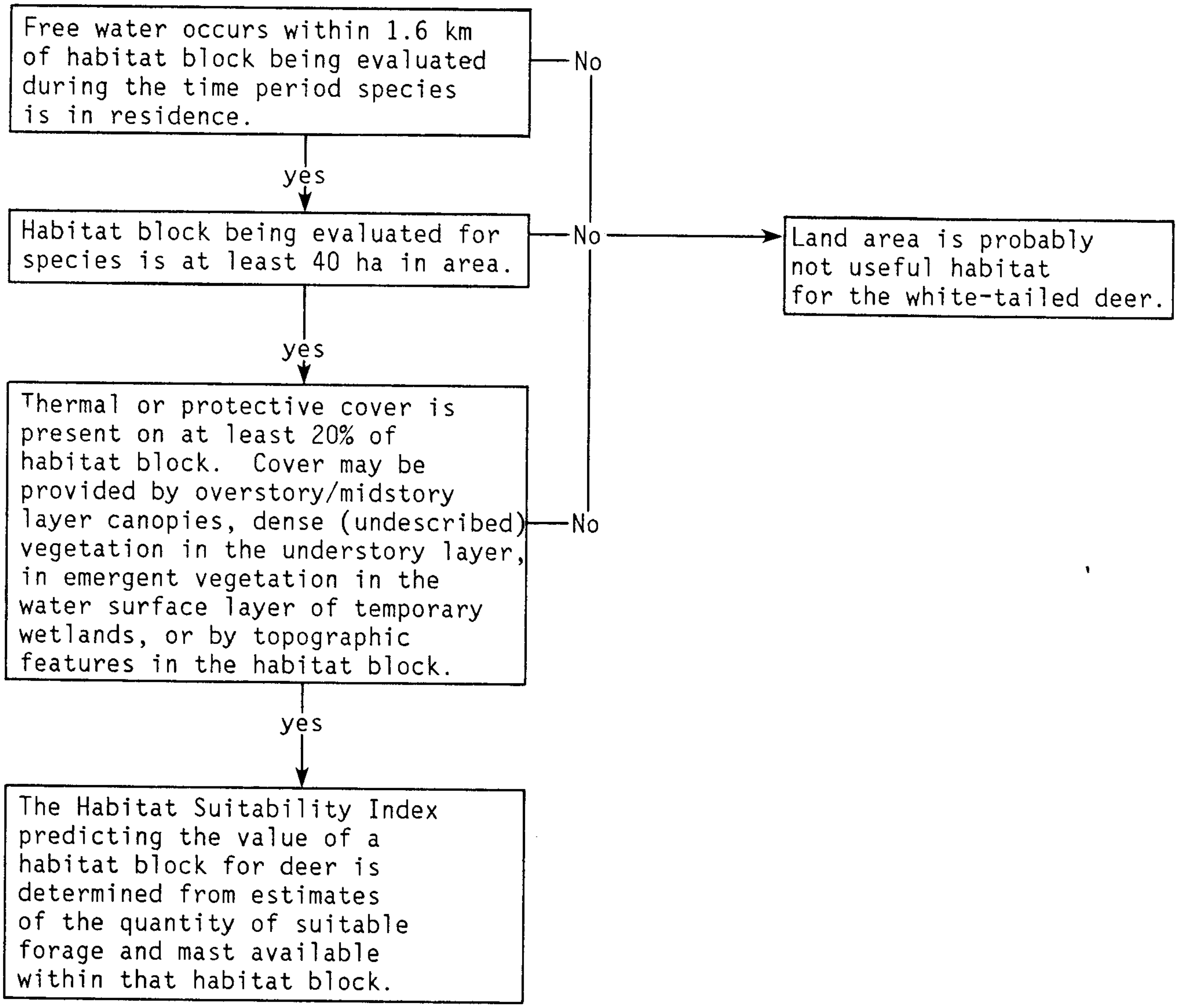

Figure 7. Logic used to develop HSI model III for white-tailed deer based on the relative quantity of suitable forage present on a hectare of habitat.

and tree mast. This estimate is imprecise because the number of sound mast items per shrub or tree varies with weather conditions when shrubs or trees trees are in flower, with the soundness of individual shrubs and trees, and with insect damage to the mast crop.

The model represented in Figure 7 is driven by surrogate values that may have relevance to measures of forage abundance (QF in Model I). If particular surrogate measures are meaningful, then model users can make decisions about habitat quality with some accuracy. Visual estimates of the quantity of cool-season herbages, evergreen leaves of woody browse plants, and edible fungi are made on randomly located plots scattered throughout the habitat, and the quantity of hard and soft mast is based on counts of the number of mast-bearing plants per unit area. Estimates of the abundance of highly digestible foodstuffs during autumn-winter within a habitat provide a basis for estimating the relative quality of that habitat for deer.

Quantities of ME per ha of habitat are predicted in Model III after estimating the weight of green cool-season grasses and forbs, evergreen leaves of woody browse plants, and of mushrooms growing on 1 m^2 sample plots located throughout the habitat block and by counting the stems of mast-producing shrubs and trees occurring within the habitat block. Plant materials with apparent digestibilities <41% are not considered in Model III and the mass of suitable forage on the experimental plots is assumed to have a digestibility of about 50%. This relatively low value is used because no effort is made in sampling to identify and distinguish individual forage items or the relative growth stage of green cool season forages. A total of about 58 kg dry matter/ha of green grasses, green forbs, evergreen leaves of woody browse plants, and mushrooms need occur within a ha of habitat to produce 100,000 kcal of ME, if one conservatively applies an average digestibility of 50% to suitable forages, assumes 4.3 kcal/g gross energy for these dried forages (above), and a digestible energy to metabolizable energy conversion factor (above) of 0.8 (58,000 g/ha x 4.3 kcal/g x 50% digestibility x 0.8 = 100,000 kcal ME/ha). Each 1 m^2 within the ha of habitat needs to provide an average of 6 g dry matter of suitable foodstuffs to provide about 100,000 kcal ME/ha.

Mast items also contribute to the metabolizable energy available to deer within a habitat. Lay (1969) reported that six species of shrubs and trees that produced fruit eaten by deer during autumn-winter produced about 1.13 kg mast/woody stem. These data may be very conservative estimates because Lay did not include oaks (*Quercus* spp.) in his listing and may not have expressed his data in terms of oven dry weights. I will use these conservative values in the following HSI calculation because I have no better data set. If the relative digestibility of mast items is 68% (above), the average gross energy value of mast items is 5.1 kcal/g (above), and if the 1.13 kg mast/stem value is relevant then about 32 stems/ha are required to produce 100,000 kcal ME/ha (32 x 1.13 = 36,130 g/ha x 5.1 kcal/g x 68% digestibility x 0.8 conversion factor = 100,000 kcal ME/ha).

A determination of the relative quality of habitat for deer during autumn-winter can be made by estimating the ME available to deer from both forages (green grass, green forbs, evergreen leaves of woody browse plants, and mushrooms) and from mast. The presumed energy content of both food sources has been scaled so that absence provides no ME and maximum values (6 g dry matter/m^2 for forages and 32 stems/ha for mast) each may provide 100,000 kcal ME to deer. These relationships for SIWF and SIWM are expressed as SI curves in Figures 8 and 9, respectively. The HSI measure is a sum of the two SI values with values greater than 1.0 rounded to 1.0.

$$HSI = SIWF \text{ (winter forage)} + SIWM \text{ (winter mast)}$$

Model IV. Predicting the presence or absence of deer on a land unit. The concept of the quantity of forage in a habitat block, which drives Models I-III, also drives Model IV. Here, forage quantity is estimated in the simplest of terms - presence or absence of major forage classes. The logic used in developing this model is shown in Figure 10. Survey plots within each hectare of habitat are examined for the presence of cool-season grasses or forbs, mast, or leafy browse. The hectare of habitat is presumed to have some value as habitat for deer if any representatives of the three forage classes occur on one-third of the sample plots. The additional steps suggesting that the presence of suitable forages on many or most plots is indicative of high-quality habitat is not made for this model, because it is difficult to translate numbers of plants into forage weights without performing the appropriate conversion steps. Model IV has some real-world relevance because some habitats, such as pole-sized pine plantations, may provide water and protective cover but essentially no useful food for deer. This condition could be predicted with Model IV.

Model IV will generally be of limited utility for evaluating habitats because it is driven by very superficial information. The model is not discussed further because I am unable to express presence or absence of forage in terms of a Habitat Suitability Index.

Comparison of models I-IV. The energetics model (Model I) is based on the abundance of different forage types occurring on a study area, the assumed digestibility of each of those forage types, the caloric content of the forages, a conversion factor that transforms estimates of digestible energy to estimates of metabolizable energy, and estimates of the energy requirements of deer. The HSI determination compares the quantity of metabolizable energy on a study area with the quantity of metabolizable energy on a standard study area. The comparison seems to represent a relative measure of the potential carrying capacity of the evaluation area for deer during the autumn-winter seasons in the Gulf of Mexico and South Atlantic coastal plains. Forage abundance clearly drives this model. Habitats with some forage, if only of minimal usefulness (forage <41% in digestibility has no usefulness) still have some utility to deer, whereas habitats with essentially no forage (even if the micro amounts present are of high digestibility) have little or no utility to deer.

Model II is based directly on Model I. The major difference in Model II is that QF, the abundance of different forage types occurring on a study area, and DF, the assumed digestibility of these forage types, are represented as Suitability Index curves in the more usual HSI format. A critical feature of

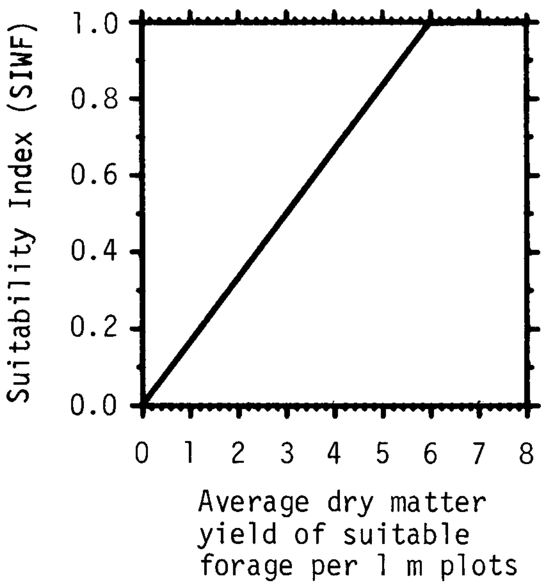

Figure 8. SI values for winter forage (WF) increase as the grams dry weight of suitable forage per 1 m^2 plots increases.

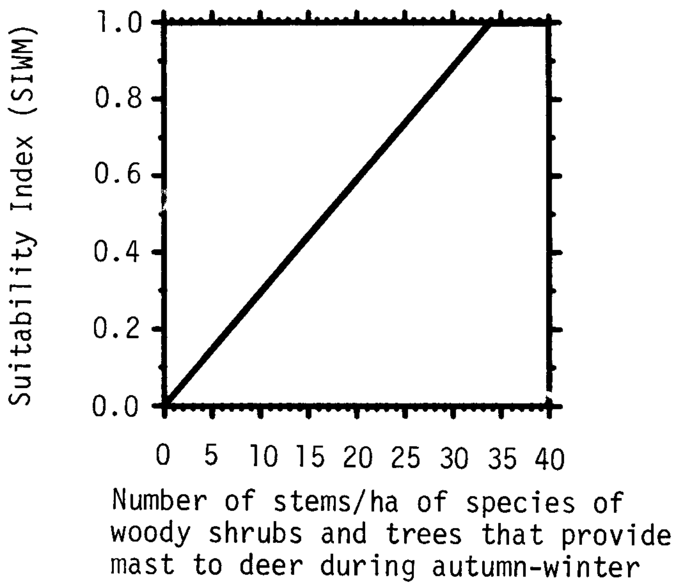

Figure 9. SI values for winter mast (WM) increase as the number of stems of suitable woody shrubs and trees increase within a hectare of habitat.

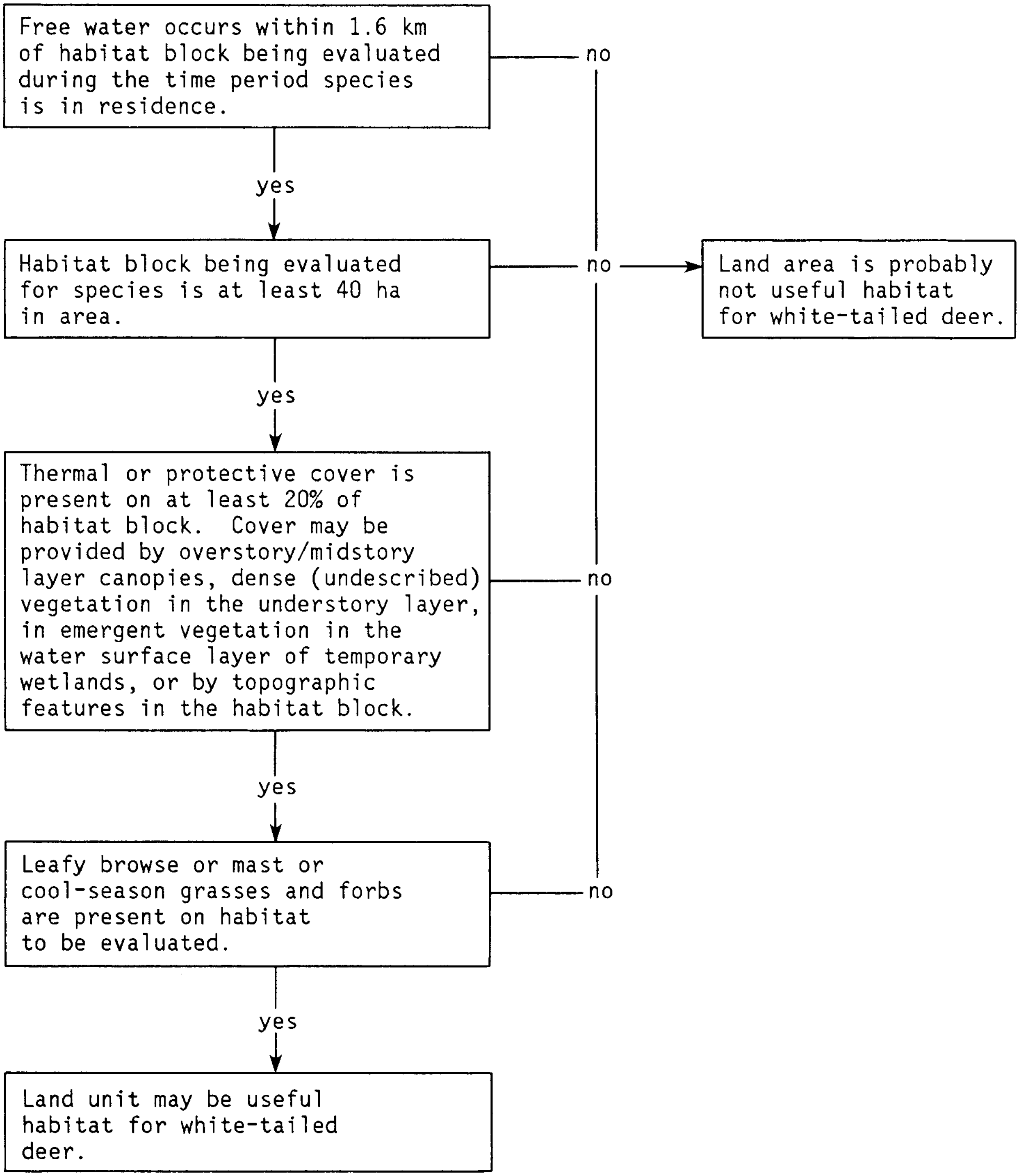

Figure 10. Logic used to develop model IV to determine the possible presence or absence of white-tailed deer on a land unit.

an HSI model, such as Model II, is the assumption that meaningful SI curves can be developed and then meaningfully combined in some logical manner to reflect the relative quality of habitats. The two related models provide a test of this assumption. HSI values are calculated for 16 different habitat configurations in Table 4 using the formats of Models I and II. HSI determinations for Model II are listed for three different combinations of the two SI curves (Figures 5 and 6) - a geometric mean, an arithmetic mean, and a simple product of the two SI curves; the three combinations of SI curves are each highly correlated with the respective HSI value from Model I ($r = 0.85 - 0.86$), but each varies disturbingly from HSI values in Model I. Nine of the HSI values calculated from the geometric mean, seven from the arithmetic mean, and nine from the simple product of the SI curves varied from their respective counterparts in Model I by >0.1 units (Table 4). Four of the values from the geometric mean calculation, three from the arithmetic mean calculation, and five from the simple product of the two SI curves varied from counterpart values in Model I by ≥0.2 units (Table 4). Especially perplexing are conditions where 75%, 50%, and 25% of the maximum forage exists on an evaluation site and this forage is all highly digestible ($SIV2 = 1.0$). The Model II HSI values for these habitat conditions should be 0.75, 0.5, and 0.25, but the geometric mean and arithmetic mean estimate the HSI values as 87% - 88%, 71% - 75%, and 50% - 63%, respectively. The geometric and arithmetic means each provided HSI estimates that were in error in 7 and 6 of the 12 instances, respectively, where only 75%, 50%, or 25% of the maximum forage amounts were present on an evaluation area (Table 4).

Model II uses SI curves instead of quantitative measures of forage abundance and forage digestibility. Comparisons between estimates of HSI values using SI curves and HSI values from Model I suggest that rules may need to be established to define: (1) how SI curves should be structured, and (2) how SI values from a number of variables should be combined to form HSI estimates.

Model III is more conservative than Model I because estimates of forage abundance are relative rather than highly quantified. Model III is still a relevant model, however, because it is based on the apparent abundance of leafy browse, mast, cool-season herbaceous growth, and edible fungi - the forage classes most likely to contribute large quantities of suitable forage to deer during autumn-winter.

Model IV, although derived from Model I, cannot be directly compared with Models I-III because it is driven by scanty and only descriptive information about the apparent presence or absence of forage classes on sample plots.

Application of the Models

Summary of model variables. There are four models for white-tailed deer described above. Each is driven by estimates of the quantity of suitable forage on a study area during autumn-winter. Biologists using these models must determine the level of resolution that is needed. Level of resolution determines the appropriate model to use and the model determines the field effort required to measure model variables. Good quantitative estimates of habitat quality for white-tailed deer can be made if great effort is expended

Table 4. A comparison of HSI values developed from Model (I) and Model (II) for 16 calculated habitat configurations.

Model I				Model II				
Quantity of suitable forage kg/ha	Apparent digestibility of forage	kcal ME/ha	HSI value	SI value for forage quantity (QF)	SI value for forage digest-tibility (DF)	HSI value geometric mean $(SIV1 \times SIV2)^{1/2}$	HSI value arith-metric mean $\frac{(SIV1 + SIV2)}{2}$	HSI value simple product (SIV1 × SIV2)
45.5	64.00	100173	1.00	1.0	1.0	1.0	1.0	1.0
45.5	58.25	91173	0.91	1.0	0.75	0.87	0.88	0.75*
45.5	52.50	82173	0.82	1.0	0.5	0.71*	0.75	0.5**
45.5	46.75	73173	0.73	1.0	0.25	0.50**	0.63*	0.25**
34.13	64.00	75141	0.75	0.75	1.0	0.87*	0.88*	0.75
34.13	58.25	68390	0.68	0.75	0.75	0.75	0.75	0.56*
34.13	52.50	61639	0.62	0.75	0.5	0.61	0.63	0.38**
34.13	46.75	54888	0.55	0.75	0.25	0.43*	0.50	0.19**
22.75	64.00	50086	0.50	0.5	1.0	0.71**	0.75**	0.50
22.75	58.25	45586	0.46	0.5	0.75	0.61*	0.63*	0.38
22.75	52.50	41087	0.41	0.5	0.5	0.50	0.5	0.25*
22.75	46.75	36587	0.37	0.5	0.25	0.35	0.38	0.13**
11.38	64.00	25054	0.25	0.25	1.0	0.50**	0.63**	0.25
11.38	58.25	22803	0.23	0.25	0.75	0.43**	0.50**	0.19
11.38	52.50	20552	0.21	0.25	0.5	0.35*	0.38*	0.13
11.38	46.75	18301	0.18	0.25	0.25	0.25	0.25	0.06*

*Estimated HSI value differs from calculated HSI value for Model I (column 4) by ≥0.1 units.

**Estimated HSI value differs from calculated HSI value for Model I (column 4) by ≥0.2 units.

to measure suitable forages on a study area. Relative estimates of habitat quality for white-tailed deer can be made with some assurance if relative estimates are made of the quantity of suitable forages on a study area. Only gross estimates, which describe the probable presence or absence of white-tailed deer on a study area, can be made, however, if only superficial surveys are conducted to determine the presence or absence of suitable forages on a study area.

The biologist, after selecting the most appropriate model, should then examine recent, high-resolution, aerial photographs of the study area. Large blocks of land without overstory or midstory cover and blocks of land that seem devoid of surface water may be areas of little or no value to deer. These land blocks may frequently consist of cultivated croplands, haylands, areas where tree harvest has recently occurred and revegetation with new tree growth has not yet occurred, and areas subjected to pressures of urbanization. Those land areas near and under overstory and midstory canopies and near sources of surface water are candidate areas for evaluation as deer habitat during autumn-winter. Descriptions of how variables for the different models are combined to determine the respective HSI values, are shown in Figure 11. The procedures used to estimate the quantity of suitable foods on a study area are described in Figure 12.

Model assumptions. These models for the white-tailed deer were developed from several data sets developed in east Texas and Louisiana. Hopefully, the models have relevance throughout the gulf and South Atlantic coastal plains. My descriptions of habitat criteria important to white-tailed deer are based on generalizations about ruminant nutrition, quantitative measures of deer physiology (mostly obtained from outside the gulf and South Atlantic coastal plains), and forage composition and digestibility estimates specific to the coastal plains. My descriptions of procedures for evaluating habitat quality will be in error if I have made incorrect judgements about kinds of data that should be used in these models or if I have misinterpreted the meaning of particular data sets.

The models are based on concepts of the energy requirements of deer. I have assumed that habitat quality can be evaluated on the basis of the energy requirements of deer and the available energy within forages. It can be argued that any carrying capacity model for deer in the coastal plains should also consider phosphorus and nitrogen requirements and availability in forages. I have restricted these models to a consideration of energy factors mainly because nitrogen and phosphorus requirements of deer are poorly known and availability in forages is expensive to measure.

I made several assumptions about the energy requirements of deer. The basal metabolic rate of southern deer was estimated from the interspecies mean metabolic rate. The activity metabolic rate of female deer during autumn-winter was estimated as 1.8 times the basal metabolic rate, and the activity metabolic rate of male deer during the rut was estimated as 2.1 times the basal metabolic rate. Values for both does and bucks are guesses. If actual activity metabolic rate requirements are greater, then the forage digestibility rates necessary to satisfy metabolic requirements may be higher than values cited in Tables 2 and 3. If actual activity metabolic rate requirements are

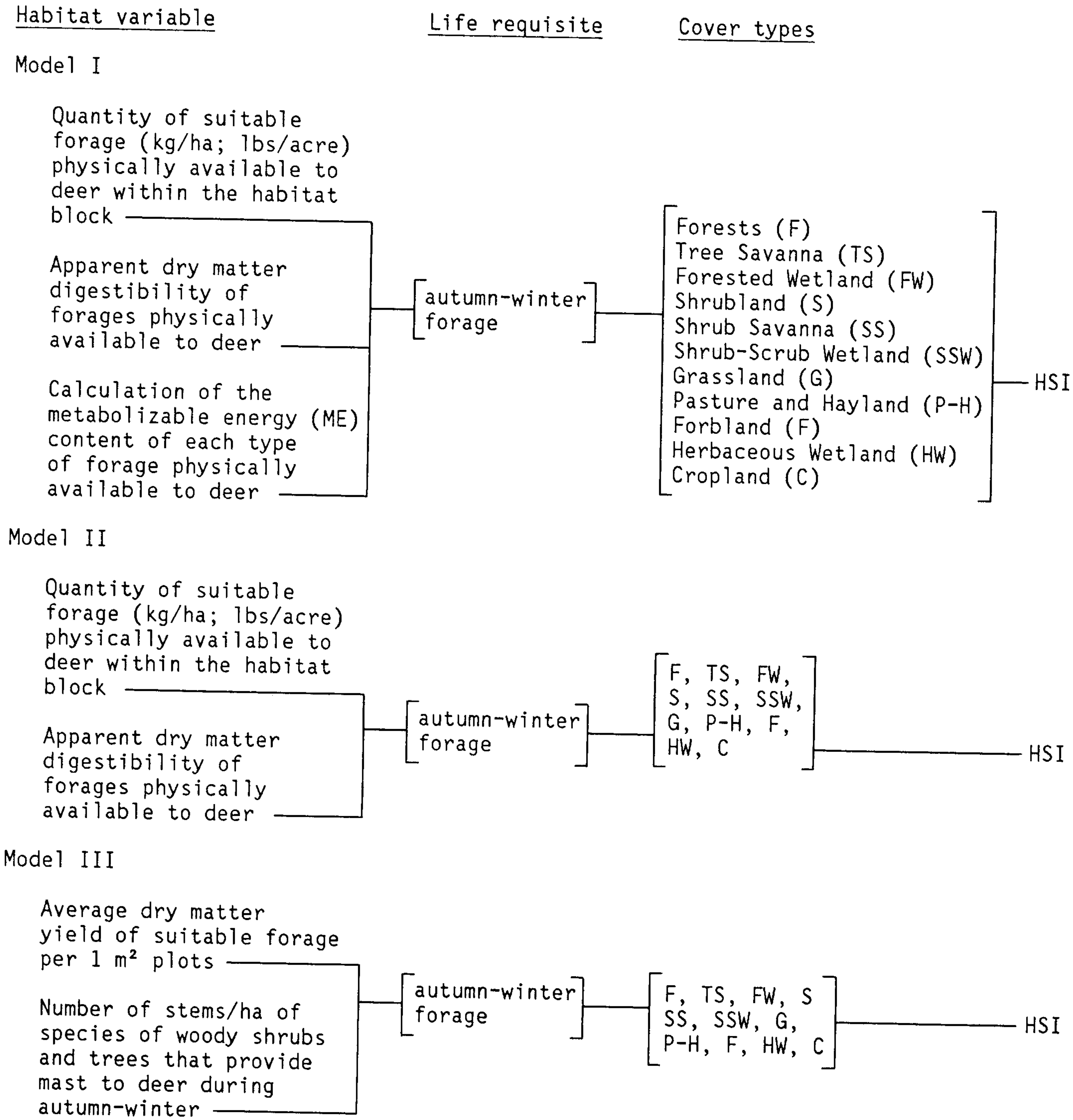

Figure 11. The relationship between habitat variables, life requisites, and cover types to autumn-winter HSI's for white-tailed deer in the gulf and South Atlantic coastal plains. Habitat variables are listed only for Models I-III because no HSI calculation is made for Model IV.

Variable (definition)	Cover type	Suggested techniques
Quantity of suitable forage (kg/ha; lbs/acre physically available to deer within the habitat block (Models I and II).	F,TS, FW, S, SS, SSW, G, P-H, F, HW, C	Establish transects and 1 m^2 sample plots along transects. Provide about 100 plots/ha. Estimate for each sample plot the weight of forage in each of the forage classes (listed for QF in Model I) that occurs from the ground surface to 1.5 m above the ground surface. Clip vegetation by forage classes in every tenth plot, oven-dry, weigh forage by forage class, and correct visual estimates of forage abundance. Obtain estimates of mast weights by establishing traps under mast producing plants and weighing collected mast or by counting and weighing a subsample of mast items.
Average dry matter yield of suitable forage per 1 m^2 plots. (Model III).		Establish transects and 1 m^2 sample plots along transects. Provide about 100 plots/ha. Make visual estimates during autumn-winter of the dry weight of evergreen leaves of woody browse plants, mushrooms, and cool-season grasses and forbs within 1.5 m of the ground on each sample plot. Determine the average dry matter yield for 1 m^2 plots and obtain relative SI values by consulting Figure 8.

Figure 12. Definitions of variables and suggested measurement techniques.

Variable (definition)	Cover type	Suggested techniques
Number of stems/ha of species of woody shrubs and trees that provide mast to deer during autumn-winter (Model III).		Obtain estimates of relative mast production by counting the number of stems/ha of species of woody shrubs and trees that provide mast to deer during autumn-winter. Determine the relative SI value for the stem count per ha by consulting Figure 9.
Leafy browse, or mast, or cool-season grasses and forbs are present on the habitat block (Model IV).		Establish transects and sample plots along transects. Provide about 100 plots/ha. Determine if leafy browse, edible fungi, cool-season grasses and forbs, or mast producing plants occur on one-third of the sample plots. If one of the four forage types does occur on one-third of the plots consider suitable deer forage present.
Apparent dry matter digestibility of forages physically available to deer (Models I and II).		Consult values for the dry matter digestibility of different classes of forages (DF) listed for Model I.
Calculation of the metabolizable energy (ME) content of each type of forage physically available to deer (Model I).		Determine if forage type is a roughage or a seed and use estimated gross energy and metabolizable energy values cited for energy values (EV) in Model I.

Figure 12. (Concluded).

lower, then forages of lesser digestibilities can be used to satisfy nutritional demands. Different activity metabolic rate values might change the classes of foods required to satisfy the metabolic energy requirements of deer. In any case, the very abundant foods, such as warm-season grasses, warm-season forbs, and woody browse twigs are likely to remain as nutritionally inadequate foods for deer in the coastal plains during autumn and winter.

Estimates of the digestible dry matter of forages were made in *in vivo* microdigestion experiments. None of the forages evaluated with the microdigestion technique was compared to true digestibility coefficients determined by digestion trials with white-tailed deer. Consequently, I have assumed that the microdigestion values do reflect the relative digestibility of selected foods. The only assurance that this assumption is correct is that the *in vivo* microdigestion values bear a significant relationship to values estimated from the summative equation (Short et al. 1974). Estimates of forage digestion suggested by the summative equation are based on relationships formulated for the way that domestic ruminants digest forages of different composition. I have also assumed that the estimated gross energy values are reasonable and that the conversion value translating digestible energy to metabolizable energy is meaningful.

Cycles of changes in body weights and food consumption rates over the annual period were developed from a limited series of feeding trials performed under controlled conditions with deer in captivity. I have assumed that results from these feeding trials reflect cycles that would also occur in wild deer.

I have assumed that the autumn-winter period is critical to the white-tailed deer in the Gulf of Mexico and South Atlantic coastal plains because the quantity of life-sustaining forage is limited at this time even though roughages of low digestibility may be in great abundance. I have further assumed that free water must be available within a radius of 1.6 km of a study site and that a block of land should be at least 40 ha to be considered potential habitat for deer. These restrictions are intended to help a biologist quickly and legitimately exclude large blocks of land that have insufficient cover and no water from consideration as deer habitat.

I assumed that I could estimate the carrying capacity of a habitat block (Model I) by estimating metabolizable energy on that habitat block and dividing that value by an arbitrary standard for metabolizable energy. I further assumed that I could express values for forage quantity (QF) and forage digestibility (DF) in Model I as standard SI curves in Model II, and that an HSI value could be determined from the geometric mean of these indices. Comparisons in Table 4 suggest that this assumption may not be entirely correct.

I have assumed that explicit measures of forage abundance like clip-weigh techniques, fruit and seed traps, and periodic mushroom surveys are useful processes for measuring the abundance of forages on a study area. I also assumed that certain surrogate measures of food abundance, such as visual estimates of forage abundance along transects and counts of mast producing plants, might bear some relationship to more quantitative measures of forage abundance, so that models with some or limited precision can be built using the surrogate measures.

SOURCES OF OTHER MODELS

Several carrying capacity models have been developed for deer and their habitats (Moen 1973; Wallmo et al. 1977; and Mautz 1978). The model developed by Wallmo et al. (1977) for mule deer in Colorado has been applied to white-tailed deer occupying the Savannah River Plant in South Carolina (Harlow 1984). Concepts in that model are similar to those in Model I, although values for individual components vary in the two models. Harlow (1984) also reviewed estimates of carrying capacity for the Savannah River Plant based on kilograms of forage available/kilograms of forage required by deer. Presumably, only useable forage (some level of digestibility) is used in making the calculation, although the level of digestibility that constitutes usefulness is not described. Harlow (1984) also described a model that estimated the carrying capacity of a habitat in Virginia on the basis of the energy available in habitats during different seasons of the year and the calculated energy requirements for a deer herd of known size. Many assumptions about the seasonal energy requirements of deer must be made to utilize the Virginia model. Other models exist that seem similar in resolution to Model IV. For example, Armbruster and Porath (1980) developed a scorecard for ranking habitat variables in a variety of deer habitat types.

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A review and synthesis of existing information were used to develop a Habitat Suitability Index (HSI) model for the white-tailed deer (Odocoileus virginianus). The model consolidates habitat use information into a framework appropriate for field application, and is scaled to produce an index between 0.0 (unsuitable habitat) and 1.0 (optimum habitat). HSI models are designed to be used with Habitat Evaluation Procedures previously deveroped by the U.S. Fish and Wildlife Service.

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