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Estimating Carrying Capacity With Simultaneous Nutritional Constraints

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Abstract

A new procedure is presented for estimating carrying capacity (the number of animals of a given species that can be supported per unit area of habitat) on the basis of two simultaneous nutritional constraints. It requires specifying the quantity (biomass) and quality (chemical composition or digestibility) of available food and the nutritional requirements of the animal species. Its application is illustrated with an example involving black-tailed deer (*Odocoileus hemionus sitkensis*) in four forest habitats during summer and winter with three sets of snow conditions and two levels of metabolic requirements for digestible energy and digestible protein. Results illustrate the fundamental importance of habitat, season, and nutritional status in determining the capability of a landscape to support animals.

Keywords: Carrying capacity, nutrition, nutritional requirements, deer, *Odocoileus hemionus*, wildlife habitat, wildlife management.

Introduction

Quantitative evaluations of habitat have become increasingly important in forest, range, and wildlife management in recent years. Many procedures for evaluating habitat have been suggested, but few have been based on nutritional relations between animals and their habitat. Carrying capacity (the number of animals that can be supported per unit area of habitat) is usually of principal concern and, by definition, is strongly dependent on both the quantity and nutritional quality of available food. Animals in natural habitats have access to many forages differing greatly in their abundance and nutritional quality. Diets selected by animals vary accordingly. The problem of simultaneously accounting for nutritional requirements and behavior of animals as well as a variety of forages differing greatly in abundance and quality has stymied attempts to derive nutritionally based estimates of carrying capacity.

Wallmo and others (1977) suggested a way to estimate carrying capacity based on forage quantity and then evaluating that estimate relative to nutritional requirements. Moen (1978) modeled nutritional requirements and dietary intake needed to meet them and, by incorporating food availability in the habitat into the model, provided a way to estimate carrying capacity. But both these procedures require that diet composition and quality be specified, and diet composition is not usually known. Even when it is known, it should be expected to change as the availability of various forages changes. In other words, it should be expected to be dependent, in part, on animal density, thus complicating the problem of estimating carrying capacity.

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Recently, Hobbs and Swift (1985) proposed a way to estimate carrying capacity explicitly incorporating nutritional requirements and not requiring diet composition to be specified. Their procedure solves for the maximum amount of biomass (kilograms per hectare) obtainable from a mixture of all forages in the habitat such that the biomass meets or exceeds a specified mean nutritional concentration (for example, of digestible energy or protein). This solution is theoretically equivalent to the amount of food consumed by the maximum number of animals the habitat could support if all the animals selected a nutritionally optimal diet meeting the given nutritional constraint. Dividing this food amount by the average daily intake of dry matter of, for example, a deer (kilograms per day per deer) yields an estimate of carrying capacity (deer days per hectare). This is clearly an upper limit and does not include other factors affecting food quality, intake, and processing or long-term effects of overgrazing. But it does provide a way to compare the relative capacities of various habitats to support animals given their present specified food resources and specified nutritional requirements. In this sense, it is a major advance over earlier methods. Like earlier methods, though, the procedure of Hobbs and Swift (1985) considers one nutritional factor at a time; for example, energy independent of protein and then protein independent of energy. A more satisfactory solution would be to consider all factors simultaneously, because nutritional constraints operate simultaneously.

We provide a way to estimate carrying capacity while meeting two nutritional constraints: dietary concentration of digestible energy and digestible protein. Our method follows the reasoning of Hobbs and Swift (1985) but differs from their procedure in several ways. Our algorithm provides an iterative solution rather than a direct solution. We have also included two additional factors: first, the constraint that no one species can comprise more than 40 percent of the total dietary biomass and, second, that only biomass greater than 25 kilograms per hectare is available for consumption. One species almost never constitutes more than 40 percent of the diet of wild deer, apparently because of the deer's need to balance a variety of nutrients and toxins in the diet (beyond the scope of our algorithm). Rates at which deer are able to harvest food drop precipitously when forage biomass is less than 25 kilograms per hectare (Wickstrom and others 1984).

The Carrying Capacity Algorithm

We defined carrying capacity as the maximum density of animals having given nutritional requirements that can be supported for a given time by a given habitat. Nutritional requirements differ with species, age, sex, body weight, and nutritional status (for example, status of body reserves on entering the given season and costs of maintenance, production, and reproduction). Both the quantity and nutritional quality of available food within a given habitat vary continuously throughout the year and even within seasons. Carrying capacity, therefore, has meaning only in the context of specified animal requirements and specified forage resources. It is purely a theoretical concept. Its practical utility is in providing a quantitative measure of the productive capacity of a habitat for animals under a specified set of circumstances.

Our algorithm calculates carrying capacity by the maximum biomass obtainable from a mixture of forages while satisfying three constraints: (1) a specified minimum concentration of digestible dry matter (or digestible energy), (2) a specified minimum concentration of digestible protein, and (3) no single species can comprise more than 40 percent of the total biomass the user can easily change the constraints to other nutritional variables or to another limit on maximum composition by any one species (to 100 percent, for example).

The algorithm has been programmed in FORTRAN for use on the Data General¹ computing system currently used by the USDA Forest Service, but it could easily be adapted to any system with similar capabilities. The program for the Data General system is in appendix 1, and the sequence of calculations can be followed there. The program can be summarized briefly (fig. 1) as follows. The required data inputs from the habitat are the plant species (or other food categories) in the habitat, along with the available biomass (kilograms per hectare) and concentrations (percentage dry weight) of digestible dry matter and digestible protein of each. The required data inputs for the animal are the dry matter intake rate (kilograms per day per animal) and the minimum dietary concentrations of digestible dry matter and digestible protein needed to meet nutritional requirements at the given rate of intake.

The maximum quantity of biomass obtainable from the habitat and satisfying all three constraints (see above) is then calculated by proceeding through the following five steps: (1) Solve for the dry matter digestibility (DMD) constraint; ignore the protein constraint. Successively add the biomass of each species, beginning with the highest and working toward the lowest DMD until the average DMD concentration of the biomass reaches the minimum constraint. Check to see if the 40-percent-maximum constraint has been exceeded; if so, reduce accordingly the amount of biomass included from that species and repeat the procedure until both the DMD and 40-percent-maximum constraints are satisfied. Then calculate protein concentration for that particular combination of biomass. (2) Repeat step 1 for protein concentration; ignore the DMD constraint. Calculate DMD for that particular combination of biomass. (3) If either step 1 or step 2 results in zero biomass, then there is no solution, and carrying capacity is zero. (4) If either step 1 or step 2 satisfies both the DMD and the protein constraint, then it is a possible solution. If only **one** of the steps satisfies both constraints, it is **the** solution. If **both** step 1 and step 2 satisfy both constraints, the greater biomass of the two is the solution. (5) If neither step 1 nor step 2 satisfies both constraints but both yield biomass greater than zero, then the solution is found by beginning with the inclusion of all species that had 100 percent of their biomass included in **both** step 1 and step 2. Additional species are added in the order of the greatest amount of biomass that can be added while still satisfying both DMD and protein constraints. When no additional biomass can be included without violating either constraint, the 40-percent-maximum constraint is checked to see if it has been violated. If it has been violated, the biomass of that species is reduced accordingly, and the procedure is repeated until all three constraints are satisfied.

After the maximum quantity of biomass (kilograms per hectare) obtainable from the habitat has been determined, 25 kilograms per hectare is subtracted (and is considered unavailable); the result is divided by the specified dry matter intake rate (kilograms per day per deer), which yields the estimate of carrying capacity (deer days per hectare). Computer output consists of all input data, the percentage of each species' biomass included in the "diet," the percentage composition of the "diet," the mean concentrations of digestible dry matter and digestible protein in the "diet," the maximum biomass, and the carrying capacity. Three sets of output are provided (appendix 2), one each for step 1, step 2, and step 5 (if necessary).

¹ The use of trade, firm, or corporation names in this publication is for the information and convenience of the reader. Such use does not constitute an official endorsement or approval by the U.S. Department of Agriculture of any product or service to the exclusion of others that may be suitable.

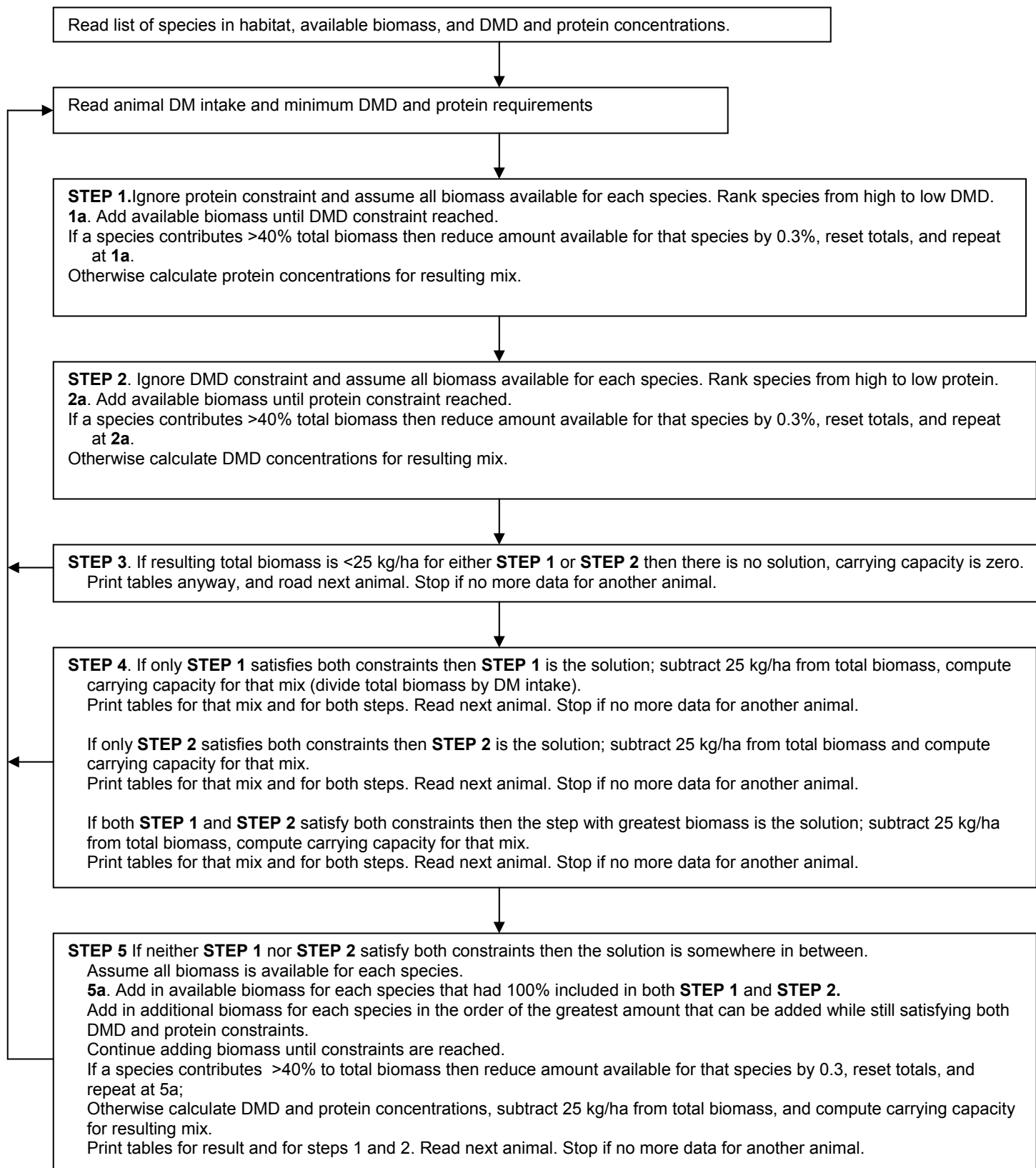


Figure 1-Flow diagram of solution process.

An Example

We used the carrying capacity algorithm to estimate carrying capacities of four hypothetical habitats for black-tailed deer (*Odocoileus hemionus sitkensis*) in southeastern Alaska. The habitats represented a broad range of forest environments during both summer and winter. We also varied the nutritional requirements of the deer.

Assumptions

The hypothetical habitats were chosen to represent (1) a commercial, old-growth, hemlock-spruce stand with about 30,000 board feet per acre (net wood volume) and 96 percent crown closure; (2) a noncommercial, old-growth, hemlock-spruce stand with about 7,000 board feet per acre and 80 percent crown closure; (3) a closed-canopy, even-aged stand with 21,000 board feet per acre and 99 percent crown closure; and (4) a 5-year-old clearcutting dominated by shrubs and hemlock and spruce saplings. Biomass values were estimated for summer (mid-July) and winter (mid-December) by using Hanley and McKendrick's (1985) work on phenological changes in forage availability and other descriptions of understory composition and biomass. We also made the following assumptions. During summer, shrub leaves are consumed, and they comprise 60 percent of the total shrub biomass (current annual growth). In winter, shrub stems are consumed, and they comprise 40 percent of the total summer shrub biomass. Evergreen forbs in commercial forests have the same biomass during winter as during summer. But in relatively open-canopied, noncommercial forests their biomass is 50 percent of that in summer (because of winter dessication), and in open clearcuttings their biomass is only 25 percent of that in summer. Availability of conifers (litterfall and low branches) and lichens (litterfall) is the same year-around and is independent of snow depth. Forbs are unavailable at 10 centimeters mean snow depth because they are buried. At less than 10 centimeters snow depth, their availability is a linear function between 0 centimeters (100 percent available) and 10 centimeters (0 percent available). Shrubs become unavailable at 60 centimeters mean snow depth because of bending and burial. At less than 60 centimeters mean snow depth, their availability is a linear function between 0 centimeters (100 percent available) and 30 centimeters (80 percent available) and between 30 centimeters and 60 centimeters (0 percent available).

We imposed three sets of snow conditions: 0, 12, and 50 centimeters mean snow depth in the open. To estimate the mean snow depth in each of the four stands during each of the three sets of snow conditions, we made the following assumptions based on the work by Hanley and Rose (1987). Stands with crown closure (measured with a spherical densiometer) greater than 95 percent and net wood volume greater than 20,000 board feet per acre have a mean snow depth 45 percent of that in the open. Stands with crown closure of 60 to 95 percent and net wood volume of 1,200 to 20,000 board feet per acre have a mean snow depth of 75 percent of that in the open. And stands with crown closure less than 60 percent or net wood volume less than 1,200 board feet per acre have a mean snow depth 100 percent of that in the open.

Table 1—Values of biomass (kg/ha) used in calculating carrying capacities of 4 habitats (A, commercial old-growth forest;^a B, noncommercial old-growth forest;^b C, closed-canopy, even-aged forest;^c and D, 5-year-old clearcutting) during summer and winter with 3 depths of snow in the open

Species	Summer ^d				Winter ^e											
					0 cm snow				12 cm snow				50 cm snow			
	A	B	C	D	A	B	C	D	A	B	C	D	A	B	C	D
<i>Kilograms per hectare</i>																
Forbs and ferns:																
<i>Cornus canadensis</i>	65	82	15	205	65	41	15	51	30	4	7	0	0	0	0	0
<i>Coptis asplenifolia</i>	14	20	4	38	14	10	4	10	6	1	2	0	0	0	0	0
<i>Dryopteris dilatata</i>	47	10	37	45	0	0	0	0	0	0	0	0	0	0	0	0
<i>Lysichiton americanum</i>	45	260	3	103	0	0	0	0	0	0	0	0	0	0	0	0
<i>Maianthemum dilatatum</i>	11	1	3	12	0	0	0	0	0	0	0	0	0	0	0	0
<i>Moneses uniflora</i>	12	0	1	0	12	0	1	0	6	0	0	0	0	0	0	0
<i>Rubus pedatus</i>	37	40	13	97	37	20	13	24	17	2	6	0	0	0	0	0
<i>Streptopus roseus</i>	7	2	1	14	0	0	0	0	0	0	0	0	0	0	0	0
<i>Tiarella trifoliata</i>	11	18	4	48	11	9	4	12	5	1	2	0	0	0	0	0
Shrubs:^f																
<i>Oplopanax horridum</i>	29	10	2	56	19	6	1	37	18	6	1	34	16	4	1	10
<i>Menziesia ferruginea</i>	22	29	1	36	14	19	1	24	14	18	1	22	12	11	1	6
<i>Vaccinium alaskensis</i>	160	262	11	534	106	175	7	356	102	165	7	328	90	105	6	95
Conifers:																
<i>Chamaecyparis nootkatensis</i>	0	12	0	0	0	12	0	0	0	12	0	0	0	12	0	0
<i>Picea sitchensis</i>	28	7	7	510	28	7	7	510	28	7	7	510	28	7	7	510
<i>Tsuga heterophylla</i>	65	52	11	835	65	52	11	835	65	52	11	835	65	52	11	835
Lichen,																
<i>Alectoria sarmentosa</i>	8	26	0	0	8	26	0	0	8	26	0	0	8	26	0	0

^a Hemlock-spruce stand with 30,000 board feet per acre (net volume) and 96 percent crown closure.

^b Hemlock-spruce stand with 7,000 board feet per acre (net volume) and 80 percent crown closure.

^c Hemlock-spruce stand with 21,000 board feet per acre (net volume) and 99 percent crown closure.

^d Values are current annual growth, measured in mid-July.

^e Values are current annual growth, measured in mid-December.

^f Values for summer are for leaves only; values for winter are for stems only.

We estimated forage availability for each of the four stands during each of the four environmental situations (table 1). Estimates of digestible dry matter and digestible protein concentrations of each species were based on work by Hanley and McKendrick (1983), Hanley and others (1987), and Robbins and others (1987) (table 2). Species-specific concentrations of digestible protein were lower in the clearcutting than in the forest stands because of the combined effects of lower concentration of crude protein and higher concentration of tannins (Hanley and others 1987). Estimates of metabolic requirements and intake were obtained from Hanley and McKendrick (1985) and chosen to represent two levels of requirements for an adult doe in both summer and winter: maintenance in summer with no fawns and with twin fawns, and maintenance after entering winter in good condition (from high-quality summer range) and poor condition (from low-quality summer range) (table 3). Animals entering winter in good condition have more body reserves to draw on and, therefore, lower nutritional requirements from their food supplies than do animals entering winter in poor condition.

Table 2—Values of digestible dry matter and digestible protein used in calculat-

Species	Digestible dry matter, all habitats ^a		Digestible protein, Forest habitats ^b		Digestible protein, 5-year-old clearcut ^c	
	Summer	Winter	Summer	Winter	Summer	Winter
Percent						
Forbs and ferns:						
<i>Cornus canadensis</i>	72.2 ^d	72.2	7.5 ^d	5.4	3.8 ^d	2.7
<i>Coptis asplenifolia</i>	62.6	71.6	7.6	4.2	4.0	1.9
<i>Dryopteris dilatata</i>	44.7	—	9.4	—	5.1	—
<i>Lysichiton americanum</i>	75.1	—	21.8	—	12.9	—
<i>Maianthemum dilatatum</i>	77.4	—	7.1	—	3.7	—
<i>Moneses uniflora</i>	69.9	65.1	6.1	7.2	—	—
<i>Rubus pedatus</i>	48.3	60.6	8.4	5.5	4.5	2.7
<i>Streptopus roseus</i>	70.0	—	14.6	—	8.4	—
<i>Tiarella trifoliata</i>	49.8	58.0	8.7	5.4	4.7	2.6
Shrubs: ^e						
<i>Menziesia ferruginea</i>	50.3	29.2	9.5	1.9	5.2	1.9
<i>Oplopanax horridum</i>	73.3	26.5	13.8	-0.7	7.9	-0.7
<i>Vaccinium alaskensis</i>	56.3 ^d	36.2	11.2 ^d	3.5	4.8 ^d	3.5
Conifers: ^f						
<i>Chamaecyparis</i>						
<i>nootkatensis</i>	47.3	47.3	1.8	1.8	—	—
<i>Picea Sitchensis</i>	28.9	28.9	1.8	1.8	1.8	1.8
<i>Tsuga heterophylla</i>	30.5	30.5	1.8	1.8	1.8	1.8
Lichen,						
<i>Alectoria sarmentosa</i> ^g	85.2	85.2	-4.4	-4.4	—	—

^a From Hanley and McKendrick (1983).

^b Estimated on the basis of crude protein (from Hanley and McKendrick 1983) and fig. 1 of Robbins and others (1987) with a 10-percent reduction due to phenolics.

^c Estimated on the basis of crude protein of plants from forest understories (Hanley and McKendrick 1983) reduced by 25 percent for high-light environment (Hanley and others 1987), and fig. 1 of Robbins and others (1987) with a 25-percent reduction due to phenolics in leaves (Hanley and others 1987); no reductions in shrub stems, conifers, or lichens.

^d From Hanley and others (1987).

^e Summer values are for leaves; winter values are for stems.

^f Year-round means (from Hanley and McKendrick 1983).

^g From Robbins (1987).

Table 3—Values of metabolizable energy requirement, dry-matter intake, and minimum dietary digestible dry matter and digestible protein used in calculating carrying capacities of forest and clearcut habitats during summer and winter for

Season and nutritional status	Metabolizable energy requirement	Dry-matter intake	Digestible dry matter	Digestible protein
	<i>Kilocalories/ day^a</i>	<i>Grams/ day^a</i>	<i>Percent^b</i>	<i>Percent^c</i>
Summer:				
Maintenance, no fawns	2,400	1,140	55	3.6
With twin fawns	4,300	1,940	58	7.3
Winter:				
From high-quality summer range	1,700	930	48	2.7
From low-quality summer range	2,100	1,000	55	2.7

^a From Hanley and McKendrick (1985).

^b Minimum dry-matter digestibility (DMD) given the specified metabolizable energy requirement (ME), the dry-matter intake (DMI), a gross energy value of 4.5 kilocalories/gram, and a metabolizable energy coefficient of 0.85: $DMD = ME \div 0.85 \div 4.5 \div DMI$ (see Hanley and McKendrick 1985).

^c Calculated from crude protein requirement (Hanley and McKendrick 1985) and fig. 1 of Robbins and others (1987).

Results

tats (fig. 2). Within the same habitat, carrying capacity ranged from as low as 0 to as high as 1,255 deer days per hectare, depending on season, snow conditions, and nutritional requirements. Even the relative relations between stands differed with the different circumstances. The relative value of the 5-year-old clearcutting during summer is particularly interesting. If only maintenance requirements are considered, the clearcutting has by far the greatest carrying capacity of the four habitats. But when lactation requirements are considered, the relative value of the clearcutting is much less with only about half the carrying capacity of the noncommercial forest. These results clearly illustrate the great importance of specifying the quantity and nutritional quality of food resources and the nutritional requirements of the animal whenever carrying capacity is being considered. Without such specifications, the term is meaningless.

The computer output also provides the user with insight for what plant species are most important in determining the carrying capacity of a specific habitat. In most of our cases, carrying capacity was limited by the quantity of available forbs that could be combined with shrubs, which were usually superabundant (relative to the nutritional constraints). Lichens, too, were very important in terms of digestible energy.

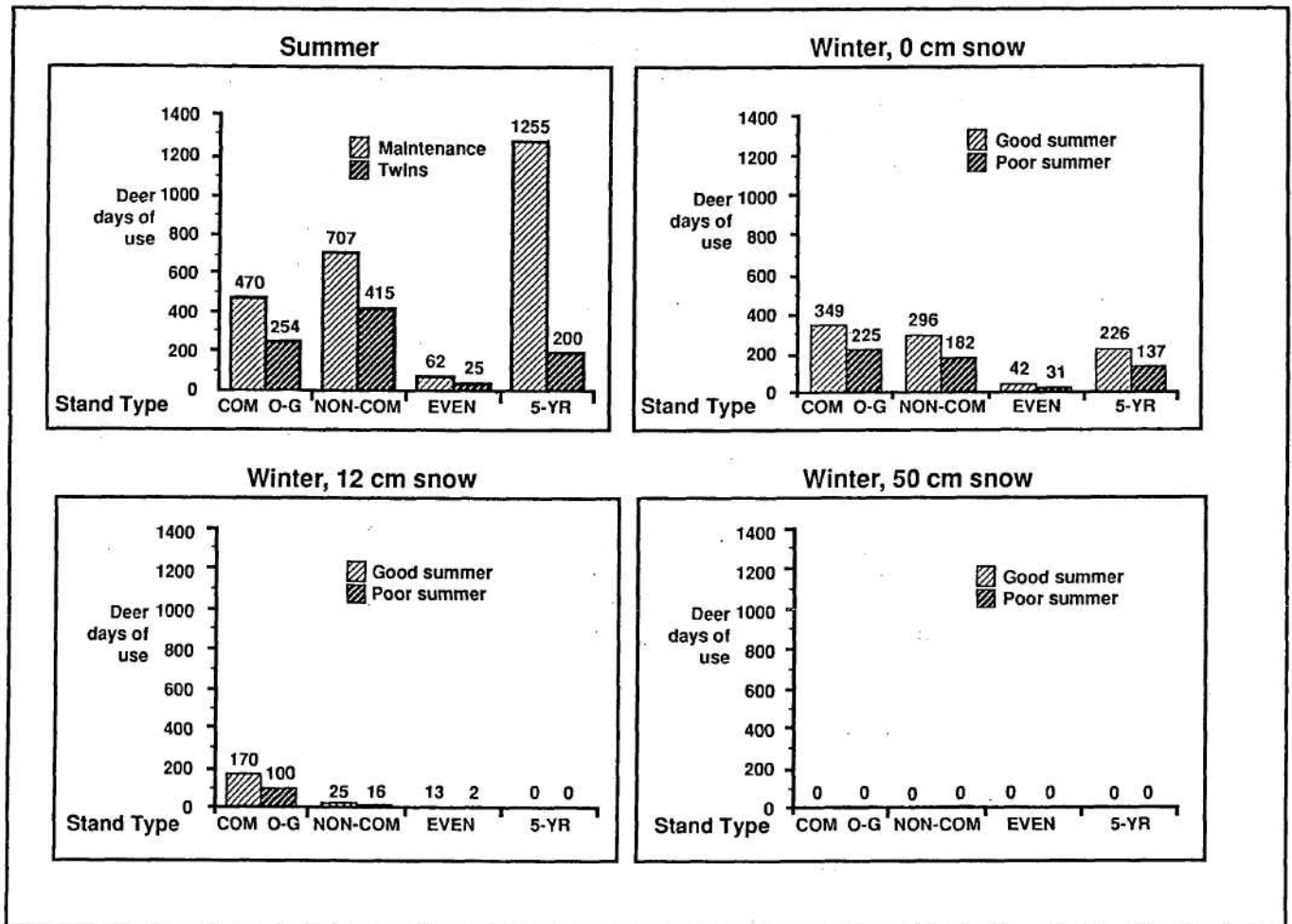


Figure 2—Estimated carrying capacities (deer days of use per hectare by adult does) of four hypothetical habitats during summer and winter with three mean snow depths in the open and two levels of metabolic requirements of the does. Values are calculated on the assumption that stated conditions remain constant throughout the entire season. COM O-G = commercial old-growth stand; NON-COM = noncommercial old-growth stand; EVEN = closed-canopy, even-aged stand; 5-YR = 5-year-old clearcutting. Good and poor summer refer to the quality of the summer range preceding use of the winter range.

It also is possible to see which nutritional factor is most limiting in any given habitat. In three cases, only the quantity of food was limiting (in other words, all the available biomass could be used while all constraints still were satisfied): the summer, commercial old-growth stand for maintenance requirements, and the summer, noncommercial old-growth stand for both maintenance and lactation. In only four cases was digestible protein more limiting than digestible energy: the summer 5-year-old stand for lactation, because of low concentrations of digestible protein, and both old-growth stands during winter with 50 centimeters of snow (for high-quality summer range in the commercial stand and both high- and low-quality summer range in the noncommercial stand), because of the availability of high-energy, low-protein lichens. In the other 25 cases, digestible energy was more limiting than was digestible protein.

It was necessary to solve simultaneously for both nutritional constraints (step 5 of the algorithm) in only 2 of the 32 analyses: the noncommercial old-growth stand during winter with 12 centimeters of snow for both the high- and low-quality summer ranges. In both cases, the simultaneous solution was much lower than the independent solutions. The simultaneous solution for the high-quality summer range was 19 deer days per hectare, while the independent solutions were 109 for digestible energy and 117 for digestible protein. For the low-quality summer range, the simultaneous solution was 0 deer days per hectare, compared to 61 and 109, respectively.

Evaluating Habitat

These results have been calculated under the assumption that the specified conditions persist for the entire season. That is why all habitats in the winter with 50 centimeters of snow yielded carrying capacities of zero. But a winter with snow persisting at such a depth would be very severe. In reality, snow depth varies throughout the winter. It is important, therefore, to provide the average available biomass of each forage through the entire winter as input data. The results are very different from those of the 50-centimeter snow in figure 2 when the input data are based on average forage availabilities for 2 months each of 0, 12, and 50 centimeters of snow (a fairly severe winter, fig. 3) (note that the results are not the same as simply averaging the carrying capacities for 0, 12, and 50 centimeters of snow from fig. 2) or 4 months of no snow and one month each at 12 and 50 centimeters of snow (a moderate winter, fig. 3).

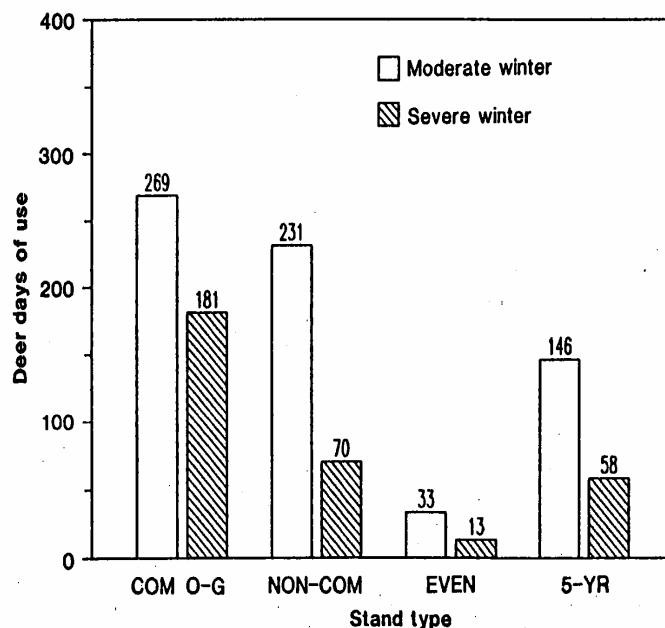


Figure 3—Estimated carrying capacities (deer days of use per hectare by adult does) of four hypothetical habitats during two different winters. The **moderate winter** is for mean snow depths in the open of 50 centimeters for 1 month, 12 centimeters for 1 month, and 0 centimeters for 4 months. The **severe winter** is for mean snow depths in the open of 50 centimeters, for 2 months; 12 centimeters for 2 months, and 0 centimeters for 2 months. Deer were assumed to have entered the winter from high-quality summer range.

These evaluations must be tempered with judgment. Even though the 5-year-old stand in figure 3 has a carrying capacity of 58 deer days per hectare in the severe winter, in reality it would be impossible for deer to survive there for 2 months in snow 50 centimeters deep; they would need to have forest habitats nearby during such time. In this sense, the estimates of carrying capacity are best considered measures of the potential a given stand has to contribute to the maintenance or productivity of a deer herd within a diverse landscape satisfying their habitat requirements.

Another important example of the need for professional judgment is evident in the cases of both old-growth stands during winter with 50 centimeters of snow (fig. 2). The carrying capacity in each case is zero because of the low availability of digestible protein, yet it could be as high as 88 in terms of digestible energy (because of the lichens). If throughout most of the winter digestible protein is superabundant and digestible energy is the limiting factor (as is the case for most of the stands in our examples), then deer could suffer a short-term protein deficit during the deep snow conditions and be benefited greatly by the lichens in the old-growth forests.

Remember that these calculations of carrying capacity are based on the assumption that all available forage satisfying the constraints is eaten. Clearly, no habitat could sustain such a high degree of use over long periods. Furthermore, if all the forage is eaten during summer, then food supplies will be greatly reduced going into winter. Therefore, if absolute estimates rather than relative estimates of carrying capacity are required, the absolute estimates should probably be reduced by at least 50 percent, and allowance should be made for habitats grazed heavily in more than one season. Long-term estimates of carrying capacity entail many complications beyond the scope of our simple algorithm.

The data sets analyzed in this example are hypothetical and were derived to illustrate the potential use of our algorithm. The analysis should not be construed as one of actual habitats or types of habitats. It was conducted only as an illustration. Every habitat is unique and must be considered on its own merits and in relation to surrounding habitats. Our algorithm merely provides one tool in the overall evaluation process.

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Appendix 1

Computer program for carrying capacity algorithm

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c Program to estimate carrying capacity with simultaneous
c nutritional constraints.
c
c The dumpfile CARRY.DMP with the program and example data sets may
c be retrieved using RIS from R10A, staff unit FSL, drawer WILDLIFE,
c folder RETRIEVAL.
c
      CHARACTER*20  SPEC(20)
      CHARACTER*40  SUB
      CHARACTER*80  TITLE
      COMMON      BIOX(20) ,dry(20) ,pro(20) ,BI040,IOPT
+      ,NSPEC,DRYF,PROF,REQUIR
      common /lim1/drypart(20),dryuse(20),biodry,drydry,digdry,drycap
+      ,prodryr,digdryr
      common /lim2/propart(20),prouse(20),biopro,drypro,digpro,procap
+      ,propror,digpror
      common /BOTH/twopart(20),twouse(20),biotwo,drytwo,protwo,twocap
+      ,protwor,digtwor
      READ(9,*)TITLE
      READ(9,*)NSPEC
      If (nspec.lt.3) stop 'There must be at least 3 species'
      BIOSUM=0
c
c read data
c
      DO  I=1,NSPEC
      READ(9,*)SPEC(I),DRY(I),PRO(I),BIOX(I)
      DRY(I)=DRY(I)/100.
      PRO(I)=PRO(I)/100.
      BIOSUM=BIOSUM+BIOX(I)
      end do
c
c 40% limit
c
      BI040=.40*BIOSUM
3 CONTINUE
c
c read limits
c
      READ(9,*,END=999) SUB,DRYF,PROF,REQUIR
      DRYF=DRYF/100.
      PROF=PROF/100.
c
c option 1 is dry matter intake is limiting
c
      IOPT=1
      CALL ONELIM (DRYF ,BIODRY,DRYDRY,DIGDRY,DRYUSE ,
+      DRYPART ,DRYCAP,PRODRYR,DIGDRYR)
c
c option 2 is protein intake is limiting
c
      IOPT=2
      CALL ONELIM (PROF ,BIOPRO,DRYPRO,DIGPRO,PROUSE ,
+      PROPART ,PROCAP,PROPROR,DIGPROR)
```

```

c
c   if either has zero carrying capacity than there is no species
c
c   mix which can satisfy the constraints
      IF (DRYCAP.EQ.0.0.OR.PROCAP.EQ. 0.)THEN
c
c   print result for dry matter constraint only
      IOPT=1
      CALL WRIT (DRYPART ,DRYUSE ,BIODRY,DRYDRY,
+               DIGDRY,DRYCAP,SPEC,SUB,TITLE)
c
c   print result for protein constraint only
      IOPT=2
      CALL WRIT (PROPART ,PROUSE ,BIOPRO,DRYPRO,
+               DIGPRO,PROCAP,SPEC,SUB,TITLE)
      ELSE
c
c   Both constraints are individually satisfied,
c   see if both constraints are also satisfied, and if so
c   see which one has highest capacity
      XMAX=0
      J=0
c
c   check dry matter option for both ratios
      IF (PRODRYR.GE.PROF-.003.AND.DIGDRYR.GE.DRYF-.003)THEN
      XMAX=BIODRY
      J=1
      END IF
c
c   check protein option for both ratios
      IF (PROPROR.GE.PROF-.003.AND.DIGPROR.GE.DRYF-.003)THEN
      IF (BIOPRO.GT.XMAX)THEN
      J=2
      END IF
      END IF
c
c   print result for dry matter constraint only
      IOPT=1
      CALL WRIT (DRYPART ,DRYUSE ,BIODRY,DRYDRY,
+               DIGDRY,DRYCAP,SPEC,SUB,TITLE)
c
c   print result for protein constraint only
      IOPT=2
      CALL WRIT (PROPART /PROUSE ,BIOPRO,DRYPRO,
+               DIGPRO,PROCAP,SPEC,SUB,TITLE)
c
c   dry matter did and was max

```

```

        IF (J.EQ.1) THEN
        IOPT=3
        CALL WRIT (DRYPART , DRYUSE , BIODRY, DRYDRY,
+                DIGDRY.DRYCAP, SPEC, SUB, TITLE)

c      protein did and was max

        ELSE IF (J.EQ.2) THEN
        IOPT=3
        CALL WRIT (PROPART , PROUSE , BIOPRO, DRYPRO,
+                DIGPRO.PROCAP, SPEC, SUB, TITLE)
        ELSE

c      neither did, solution is in between, call a two limit routine
c      for now print both results

        IOPT=3
        iwrit=1
        CALL TWOLIM (BIOTWO, PROTWO, DIGTWO, TWOUSE ,
+                TWOPART , TWOCAP, PROTWOR, DIGTWOR, iwrit)
        if(iwrit.eq.1) then
        CALL WRIT (TWOPART , TWOUSE , BIOTWO, PROTWO,
+                DIGTWO, TWOCAP, SPEC, SUB, TITLE)
        END IF
        END IF
        END IF

c      read another set of constraints

        GO TO 3

C--
999      write (12,1000)
1000     format(/, ' End of options')
        STOP
        END
        SUBROUTINE WRIT (PART, PUSE, BIOTRY, PROTRY,
+                DIGTRY, BIOCAP, SPEC, SUB, TITLE)
        REAL      PART(20), PUSE(20)
        CHARACTER*20 SPEC(20)
        CHARACTER*40 SUB
        CHARACTER*80 TITLE
        COMMON    BIOX(20) , dry(20) , pro(20) , BIO40, IOPT
+                , NSPEC, DRYF, PROF, REQUIR

c      write header for dry matter consraint

        IF (IOPT.EQ.1.OR.IOPT.EQ.3) THEN
        WRITE(12,500) TITLE, SUB , REQUIR
500      FORMAT(1H1, //, 7X, A80, //, 7X, A40, ' DRY MATTER INTAKE IS ',
+      F6.2, ' KG/DAY')
        WRITE(12,499)

c      write header for protein consraint

        ELSE IF (IOPT.EQ.2) THEN
        WRITE(12,499)

```

```

499      FORMAT
+      (//,7X,'SPECIES'
+ ,15X,'DIGESTIBLE    DIGESTIBLE    AVAILABLE    PERCENT    PERCENT OF'
+ ,/
+ ,29X,'DRY MATTER    PROTEIN    BIOMASS    USED    TOTAL'
+ ,/)
      END IF

c      write species lines for the option

      WRITE(12,501) (SPEC(I), DRY(I)*100., PRO(I)*100., BIOX(I)
+ , PART(I)*100. , PUSE(I)*100., I=1, NSPEC)
501      FORMAT(7X,A20,6X,F6.1,8X,F6.2,6X,F7.1,3X,F8.1,6X,F7.1)
      WRITE(12,502)
502      FORMAT( //,6X,
+      ' DIGESTIBLE    DIGESTIBLE    MAXIMUM    MEAN    CARRYING'
+ ,/.6X
+ , ' DRY MATTER    PROTEIN    BIOMASS    CONCENTRATION    CAPACITY'
+ ,/,6X
+ , '    REQUIRED    REQUIRED    DDM    DP    ',/)

c      set constraint to be printed

      IF (IOPT.EQ.1) THEN
      X=DRYF*100.
      Y=-10000.
      ELSE IF (IOPT.EQ.2) THEN
      X=-10000.
      Y=PROF*100.
      ELSE
      X=DRYF*100.
      Y=PROF*100.
      END IF

c      compute ratios for constraint

      IF(BIOTRY.GT.0.) THEN
      PROR=PROTRY/BIOTRY
      DIGR=DIGTRY/BIOTRY
      ELSE
      PROR=0.
      DIGR=0.
      END IF

c      write the summary line

      WRITE(12,503) X,Y ,BIOTRY,    DIGR*100.
+ ,    PROR*100., BIOCAP
503      FORMAT(11X, F6.1, 8X,F6.1,3X, F8.0, 3X, F5.2,4X,F5.2, 4X, F8.2)
C--
C--
      RETURN
      END
      SUBROUTINE ONELIM (XLIM,BIOTRY, PROTRY,
+      DIGTRY,PUSE,PART,BIOCAP,PROR,DIGR)
      REAL    PLEFT(20),PUSE(20) ,BIOLIM(20) ,BIOUS(20) ,PART(20)

```

```

      real OLDDRY,OLDPRO ,PLIM(20)
      CHARACTER*20 SPEC(20)
      CHARACTER*40 SUB
      CHARACTER*80 TITLE
      COMMON   BIOX(20) ,dry(20) ,pro(20) ,BI040,IOPT
+                                     ,NSPEC,DRYF,PROF.REQUIR

c      set limits for the option

6      DO   I=1,NSPEC
          IF (IOPT.EQ.1) THEN
              PLIM(I)=DRY(I)
          ELSE IF (IOPT.EQ.2) THEN
              PLIM(I)=PRO(I)
          ELSE
              STOP 'PLIM SETUP'
          END IF

c      biox is total biomass for each species
c      bio40 is 40% of sum of total

          BIOLIM(I)=BIOX(I)
          IF (BIOLIM(I).GT.BIO40+.001 )BIOLIM(I)=BI040
          end do
          ITER=0

c      begin iteration

4      CONTINUE

c      init total biomass used, protein used, digest dry matter used

          BI0TRY=0
          PR0TRY=0
          DIGTRY=0

c      initialize amt left to use, amt used, amt left and
c      fractional part used of biomass avail for species (biox)

          DO I=1,NSPEC
              PLEFT(I)=BIOLIM(I)
              BIOUS(I)=0
              PUSE(I)=0
              PART(I)=0
          end do

c

C      ADD IN EVERYTHING WHICH MEETS constraining CONDITION

          ILEFT=NSPEC

c

          DO   I=1,NSPEC
              IF (PLIM(I).GE.XLIM) THEN
                  ILEFT=ILEFT-1

```

```

        BIOUS(I)=BIOUS(I)+BIOLIM(I)
        PLEFT(I)=0.
        BIOTRY=BIOTRY+BIOLIM(I)
        DIGTRY=DIGTRY+BIOLIM(I)*DRY(I)
        PROTRY=PROTRY+BIOLIM(I)*PRO(I)
    END IF
end do

C--NOW SEE HOW MUCH EACH REMAINING CAN CONTRIBUTE
C--
C--
C--COMPUTE OLD RATIOS
C--
162      J=0
C--
C--FIND HIGHEST VALUE
C--
C--
        CHK=-500.
        DO      I=1, NSPEC
            IF (PLIM(I).GT.CHK.AND.PLEFT(I).GT.O.) THEN
                J=I
                CHK=PLIM(I)
            END IF
        end do
C--
C--ADD IN THE SPECIES J WHICH HAS HIGHEST LIMIT
C--
        IF (J.GT.O) THEN
C--
C--
            IF (BIOTRY.GT.0.) THEN
                OLDDRY=DIGTRY/BIOTRY
                OLDPRO=PROTRY/BIOTRY
C
            ELSE
                OLDDRY=0.
                OLDPRO=0.
            END IF
C
        IF (IOPT.EQ.1) THEN
C
            XTRY=DIGTRY
            ELSE
                XTRY=PROTRY
            END IF
C
        IF (PLIM(J).LT.XLIM) THEN

```

```

PD=ABS ( (BIOTRY*XLIM-XTRY) / (PLIM(J)-XLIM) )

c

ELSE
PD=PLEFT(J)
END IF

c COMPUTE additions to total used, left etc

PD=AMIN1 (PLEFT(J),PD)
BIOTRY=BIOTRY+PD
DIGTRY=DIGTRY+PD*DRY(J)
PROTRY=PROTRY+PD*PRO(J)
BIOUS(J)=BIOUS(J)+PD
PLEFT(J)=PLEFT(J)-PD
END IF

c compute new ration if used is greater than zero

IF(BIOTRY.GT.0.) THEN
PROR=PROTRY/BIOTRY
DIGR=DIGTRY/BIOTRY

c otherwise zero them

ELSE
PROR=0.
DIGR=0.
END IF

c set correct limit for comparison

IF(IOPT.EQ.1) THEN
XRAT=DIGR
ELSE
XRAT=PROR
END IF

c see if limit has been reached

IF (XRAT.GT.XLIM+.0001) THEN

c has not been reached yet, see if there are more species to use
c if there are try to add some more

ILEFT=ILEFT-1
IF(ILEFT.GT.0) GO TO 162
END IF

c limit was reached, see if it is acceptable
c CHECK THE 40% OF TOTAL LIMIT PER SPECIES,
c ALSO DRY & PROTEIN REQUIRED

c CHECK FOR DIGESTIBLE DRY MATTER

```

```

c      first see if it is spinning wheels on impossible case

      IF (ITER.GT.1000) THEN
      IF (BIOTRY.LT.0.01) THEN
      BIOTRY=0
      ITER=2000
      END IF
      END IF

c

      IFAIL=0

C      for each species compute part used of total

      DO      I=1, NSPEC
      IF (BIOTRY.GT.0.) THEN
      PUSE(I)=BIOUS(I)/BIOTRY
      ELSE
      PUSE(I)=0.
      END IF

c      also compute part used of species biomass

      IF (BIOX(I).GT.0.) THEN
      PART(I)=BIOUS(I)/BIOX(I)
      ELSE
      PART(I)=0.
      END IF

c      see if the part used of total is > 40%
c      if it is then reduce the limit which can be used for species
c      and try again if under iter limit

      IF (PUSE(I).GT.0.4005) THEN
      IF (PUSE(I).LT.0.45) THEN
      BIOLIM(I)=.997*BIOLIM(I)
      ELSE IF (PUSE(I).LT.0.5) THEN
      BIOLIM(I)=.985*BIOLIM(I)
      ELSE
      BIOLIM(I)=.97*BIOLIM(I)
      END IF
      IFAIL=1
      END IF
      end do

c      check iteration limit

      ITER=ITER+1
      IF((ITER.LT.2000).AND. (IFAIL.GT.0) )GO TO 4

c      it is an okay solution, store results

      IF (BIOTRY.GT.0.) THEN
      PROR=PRQTRY/BIOTRY
      DIGR=DIGTRY/BIOTRY

```

```

ELSE
PROR=0.
DIGR=0.
END IF
BIOCAP=AMAX1 (BIOTRY-25.,0.) /REQUIR
C--
RETURN
END
SUBROUTINE TWOLIM (BIOTRY,PROTRY,
+   DIGTRY,PUSE,PART,BIOCAP,PROR,DIGR,iwrit)
REAL   PUSE(20) ,BIOLIM(20),BIOUS(20),PART(20)
real   OLDDRY,OLDPRO ,pmax(20),pmin(20),btry(0:20)
COMMON   BIOX(20) ,dry(20) ,pro(20) ,BI040,IOPT
+   ,NSPEC,DRYF,PROF,REQUIR
common /lim1/drypart(20),dryuse(20),biodry,drydry,digdry.drycap
+   ,prodryr,digdryr
common /Lim2/propart(20),prouse(20),biopro,drypro,digpro,procap
+   ,propror,digpror
integer NC(20) ,spcnum(8),nf(8),itrlim(8)
data itrlim/500,200,60,28,15,9,7,6/
C
do i=1,8
spcnum(i)=0
end do
C
c   for each constraint, find which species have = amounts.
c   These are not constraining
c   Mark those which are constraining, and set limits on possible
    ichk=0
6   DO   I=1,NSPEC
    IF (int(drypart(i)*100.+0.1).eq.int(propart(i)*100.+0.1))then
    NC(I)=0
    biolim(I)=drypart(i)*biox(i)
    else
    if ((drypart(i).gt.0).OR.(propart(i).gt.0))then
    ichk=ichk+1
    NC(i)=1
    spcnum(ichk)=i
    pmax(i)=amax1(drypart(i),propart(i))*biox(i)
    pmin(i)=0
    biolim(i)=pmax(i)
    else
    nc(i)=0
    pmax(i)=0.
    pmin(i)=0.
    biolim(i)=0.
    end if
    end if
    end do
    ITER=0
4   CONTINUE
C
c   ichk is counter for number of species to adjust, see if > 0
C
    if (ichk.eq.0) then

```

```

        STOP 'In twolim species to adjust=0'
        else if (ichk.gt.8) then
        stop 'In twolim species to adjust more than 8'
        END IF
        BIOTRY=0
        PROTRY=0
        DIGTRY=0
1      CONTINUE
C--
C--Add in all which seems not to be limiting. For non constraining
C--species use all up to upper limit. For other species use minimum.
C--
        btry(0)=0.
        DO      I=1, NSPEC
        PUSE(I)=0
        PART(I)=0
        IF (nc(I).eq.0) THEN
        BIOUS(I)=BIOLIM(I)
        BIOTRY=BIOTRY+BIOLIM(I)
        DIGTRY=DIGTRY+BIOLIM(I)*DRY(I)
        PROTRY=PROTRY+BIOLIM(I)*PRO(I)
        else
        bious(i)=pmin(i)
        biotry = biotry+pmin(i)
        DIGTRY=DIGTRY+pmin(I)*DRY(I)
        PROTRY=PROTRY+pmin(I)*PRO(I)
        END IF
        btry(i)=bious(i)
        end do
C
c Set iteration limits
c
        niters=itrlim(ichk)
        do i=1,8
        if (i.le.ichk) then
        nf(i)=niters
        else
        nf(i)=0
        endif
        end do
C--
C--Set species numbers and increments for constraining species
C--
        i1=spcnum(1)
        i2=spcnum(2)
        i3=spcnum(3)
        i4=spcnum(4)
        i5=spcnum(5)
        i6=spcnum(6)
        i7=spcnum(7)
        i8=spcnum(8)
        D1=(pmax(i1)-pmin(i1)) / NITERS
        D2=(pmax(i2)-pmin(i2)) / NITERS
        D3=(pmax(i3)-pmin(i3)) / NITERS
        D4=(pmax(i4)-pmin(i4)) / NITERS
        D5=(pmax(i5)-pmin(i5)) / NITERS

```

```

D6=(pmax(i6)-pmin(i6)) / NITERS
D7=(pmax(i7)-pmin(i7)) / NITERS
D8=(pmax(i8)-pmin(i8)) / NITERS

c
c See if initial estimate from adding minimum values satisfies the
c protein and dry matter constraints. If so it is valid initial
c maximum. Otherwise set initial maximum to zero.
c
      bmax = biotry
      promax=protry
      dmax=digtry
      iwrit=1

c
      write (*,*) ' Working on iteration •,iter

c
c Begin nested do loop search for maximum. This handles up to eight
c constraining species. Expect long run times for the larger number of
c constraining species.
c
c Species 1
c
      do j1=0,nf(1)
      n1=j1
      b1=j1*d1
      dig1=b1*dry(i1) + digtry
      pro1=b1*pro(i1) + protry
      b1=j1*d1 + biotry

c
c Species 2
c
      do j2=0,nf(2)
      n2=j2
      if (j2.gt.0) then
      b2=j2*d2
      dig2=b2*dry(i2) + dig1
      pro2=b2*pro(i2) + pro1
      b2=j2*d2 + b1
      else
      b2=b1
      dig2=dig1
      pro2=pro1
      end if

c
c Species 3
c
      do j3=0,nf(3)
      n3=j3
      if (j3.gt.0) then
      b3=j3*d3
      dig3=b3*dry(i3) + dig2
      pro3=b3*pro(i3) + pro2
      b3=j3*d3 + b2
      else
      b3=b2
      dig3=dig2
      pro3=pro2

```

```

        end if
c
c Species 4
c
        do j4=0,nf(4)
        n4=j4
        if (j4.gt.0) then
        b4=j4*d4
        dig4=b4*dry(i4) + dig3
        pro4=b4*pro(i4) + pro3
        b4=j4*d4 + b3
        else
        b4=b3
        dig4=dig3
        pro4=pro3
        end if
c
c Species 5
c
        do j5=0,nf(5)
        n5=j5
        if (j5.gt.0) then
        b5=j 5*d5
        dig5=b5*dry(i5) + dig4
        pro5=b5*pro(i5) + pro4
        b5=j5*d5 + b4
        else
        b5=b4
        dig5=dig4
        pro5=pro4
        end if
c
c Species 6
c
        do j6=0,nf(6)
        n6=j 6
        if (j6.gt.0) then
        b6=j6*d6
        dig6=b6*dry(i6) + dig5
        pro6=b6*pro(i6) + pro5
        b6=j6*d6 + b5
        else
        b6=b5
        dig6=dig5
        pro6=pro5
        end if
c
c Species 7
c
        do j7=0,nf(7)
        n7=j7
        if (j7.gt.0) then
        b7=j7*d7
        dig7=b7*dry(i7) +
        dig6
        pro7=b7*pro(i7) + pro6
        b7=j7*d7 + b6

```

```

        else
        b7=b6
        dig7=dig6
        pro7=pro6
        end if
c
c Species 8
c
        do j8=0,nf(8)
        n8=j8
        if (j8.gt.0) then
        b8=j 8*d8
        dig8=b8*dry(i8) + dig7
        pro8=b8*pro(i8) + pro7
        b8=j8*d8 + b7
        else
        b8=b7
        dig8=dig7
        pro8=pro7
        end if
c
c See if this is new maximum. If so does it satisfy constraints.
c If so save this maximum.
c
        if (b8.gt.bmax) then
        pror = pro8/b8
        if (pror.ge.prof) then
        digr = dig8/b8
        if (digr.ge.dryf) then
        btry(i1)=bious(i1) + N1*d1
        if(btry(i1)/b8.1e.404)then
        btry(i2)=bious(i2) + N2*d2
        if(btry(i2)/b8.1e.404)then
        btry(i3)=bious(i3) + N3*d3
        if(btry(i3)/b8.1e.404)then
        btry(i4)=bious(i4) + N4*d4
        if(btry(i4)/b8.1e.404)then
        btry(i5)=bious(i5) + N5*d5
        if(btry(i5)/b8.1e.404)then
        btry(i6)=bious(i6) + N6*d6
        if(btry(i6)/b8.1e.404)then
        btry(i7)=bious(i7) + N7*d7
        if(btry(i7)/b8.1e.404)then
        btry(i8)=bious(i8) + N8*d8
        if(btry(i8)/b8.1e.404)then
        iwrit=1
        promax=pro8
        dmax=dig8
        bmax=b8
        end if
        end if
        end if
        end if
        end if
        end if
        end if
        end if

```

```

        end if

        end if
        end if
        end if
C
        end do
        end do
        end do
        end do
        end do
        end do
        end do
        end do

C
C See if it found a new maximum. If so set biotry to this value.
C If not and iterations remain set the max values for dry matter and
C protein to initial values. Otherwise print message and quit.
C
        IF (BMAX.GT.0.001) THEN
        biotry=bmax
        DIGTRY=dmax
        PROTRY=promax
        ELSE
        write(12,*)
        write(12,*) ' ##### There is no solution to combined problem'
        iwrit=0
        return
        END IF

C
C CHECK THE 40% OF TOTAL LIMIT PER SPECIES. If it is violated reduce the
C upper limit and try again. If it is violated by a non-constraining
C species then add that species in as a constraining species.
C
        IFAIL=0
        DO      I=4, NSPEC
        bious(i)=btry(i)
        PUSE(I)=BIOUS(I)/BIOTRY
        IF (BIOX(I).GT.0.) THEN
        PART(I)=BIOUS(I)/BIOX(I)
        ELSE
        PART(I)=0.
        END IF
        IF ((PUSE(I).Gt.0.404)) THEN
        if(nc(i).eq.0) then
        ichk=ichk+1
        spcnum(ichk)=i
        nc(i)=1
        nf(ichk)=niters
        end if
        pmax(i)=.39*biotry
        biolim(i)=*pmax(i)
        pmin(i)=0
        iwrit=0
        END IF

```

```

        END DO
C
C   If there are iterations left try again
C
        ITER=ITER+1
        IF((ITER.LT.10).AND.(IFAIL.GT.0))GO TO 4
C
C   SUMMARIZE
C
        if (iwrit.eq.0)then
write(12,*) ' ..... '
write(12,*) ' There is no solution to combined problem'
        return
        end if
C
        IF(BIOTRY.GT.0.)THEN
digtry=dmax
protry=promax
PROR=PROTRY/BIOTRY
DIGR=DIGTRY/BIOTRY
        ELSE
        iwrit=0
        PROR=0.
        DIGR=0.
        END IF
        BIOCAP=AMAX1(BIOTRY-25.,0.)/REQUIR
C--
        RETURN
        END

```

Appendix 2

Sample of computer output

NONCOMMERCIAL OLD-GROWTH FOREST--WINTER, 12 CM SNOW
GOOD SUMMER DRY MATTER INTAKE IS .93 KG/DAY

SPECIES	DIGESTIBLE DRY MATTER	DIGESTIBLE PROTEIN	AVAILABLE BIOMASS	PERCENT USED	PERCENT OF TOTAL
CORNUS CANADENSIS	72.2	5.40	4.0	100.00	3.17
COPTIS ASPLENIIFOLIA	71.6	4.20	1.0	100.00	.79
RUBUS PEDATUS	60.6	5.50	2.0	100.00	1.59
TIARELLA TRIFOLIATA	58.0	5.40	1.0	100.00	.79
OPLOPANAX HORRIDUM	26.5	-.70	6.0	.00	.00
MENZIESIA FERRUGINEA	29.2	1.90	18.0	.00	.00
VACCINIUM ALASKENSIS	36.2	3.50	165.0	30.38	39.78
CHAMAECYPERIS NOOTKA	47.3	1.80	12.0	100.00	9.52
PICEA SITCHENSIS	28.9	1.80	7.0	.00	.00
TSUGA HETEROPHYLLA	30.5	1.80	52.0	57.47	23.72
ALLECTORIA SARMENTOS	85.2	-4.40	26.0	100.00	20.63

DIGESTIBLE DRY MATTER REQUIRED	DIGESTIBLE PROTEIN REQUIRED	MAXIMUM BIOMASS	MEAN CONCENTRATION DDM	DP	CARRYING CAPACITY
48.0	*****	126.	48.0	1.4	108.61

SPECIES	DIGESTIBLE DRY MATTER	DIGESTIBLE PROTEIN	AVAILABLE BIOMASS	PERCENT USED	PERCENT OF TOTAL
CORNUS CANADENSIS	72.2	5.40	4.0	100.00	3.00
COPTIS ASPLENIIFOLIA	71.6	4.20	1.0	100.00	.75
RUBUS PEDATUS	60.6	5.50	2.0	100.00	1.50
TIARELLA TRIFOLIATA	58.0	5.40	1.0	100.00	.75
OPLOPANAX HORRIDUM	26.5	-.70	6.0	.00	.00
MENZIESIA FERRUGINEA	29.2	1.90	18.0	100.00	13.48
VACCINIUM ALASKENSIS	36.2	3.50	165.0	32.28	39.90
CHAMAECYPERIS NOOTKA	47.3	1.80	12.0	100.00	8.99
PICEA SITCHENSIS	28.9	1.80	7.0	100.00	5.24
TSUGA HETEROPHYLLA	30.5	1.80	52.0	67.77	26.39
ALLECTORIA SARMENTOS	85.2	-4.40	26.0	.00	.00

DIGESTIBLE DRY MATTER REQUIRED	DIGESTIBLE PROTEIN REQUIRED	MAXIMUM BIOMASS	MEAN CONCENTRATION DDM	DP	CARRYING CAPACITY
*****	2.7	134.	36.2	2.7	116.67

NONCOMMERCIAL OLD-GROWTH FOREST--WINTER, 12 CM SNOW
GOOD SUMMER

DRY MATTER INTAKE IS .93 KG/DAY

SPECIES	DIGESTIBLE DRY MATTER	DIGESTIBLE PROTEIN	AVAILABLE BIOMASS	PERCENT USED	PERCENT OF TOTAL
CORNUS CANADENSIS	72.2	5.40	4.0	100.00	9.37
COPTIS ASPLENIIFOLIA	71.6	4.20	1.0	100.00	2.34
RUBUS PEDATUS	60.6	5.50	2.0	100.00	4.69
TIARELLA TRIFOLIATA	58.0	5.40	1.0	100.00	2.34
OPLOPANAX HORRIDUM	26.5	-.70	6.0	.00	.00
MENZIESIA FERRUGINEA	29.2	1.90	18.0	.00	.00
VACCINIUM ALASKENSIS	36.2	3.50	165.0	10.15	39.24
CHAMAECYPERIS NOOTKA	47.3	1.80	12.0	100.00	28.12
PICEA SITCHENSIS	28.9	1.80	7.0	.00	.00
TSUGA HETEROPHYLLA	30.5	1.80	52.0	5.86	7.14
ALLECTORIA SARMENTOS	85.2	-4.40	26.0	11.08	6.75

DIGESTIBLE DRY MATTER REQUIRED	DIGESTIBLE PROTEIN REQUIRED	MAXIMUM BIOMASS	MEAN CONCENTRATION DDM	MEAN CONCENTRATION DP	CARRYING CAPACITY
48.0	2.7	43.	48.1	2.7	19.00

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