NUTRITIONAL MODELING OF MULE DEER:

A POTENTIAL TECHNIQUE FOR THE ASSESSMENT OF HABITAT QUALITY AND CARRYING CAPACITY

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ABSTRACT.

Based upon the literature on North American deer, a nutritional model was developed for mule deer (*Odocoileus hemionus*) which examines deer requirements for protein, energy, and phosphorus. Vegetation biomass, vegetation nutrient content, and mule deer diets, as indicated by fecal analysis, were measured on two deer ranges (Duck Creek Basin and Badger Mountain) in Nevada. The calculated requirements were compared to the ability of the habitat to supply these nutrients, and surplus nutrients obtained by deer were assumed to be utilized for fawn production. Fawn production calculated could then be compared to observed fawn production to determine the adequacy of the model.

Results indicate that the model developed is inadequate in several respects, but may be suitable for determining limiting habitat factors and relative habitat quality. Duck Creek deer produced 97 fawns per 100 does in 1978, while model results predicted that only 50 fawns per 100 does could be produced. On Badger Mountain, observed fawn production was 57ff:100 dd, while predicted fawn production was 10ff:100 dd. The resulting underestimation of habitat quality was thus 55% and 84% for Duck Creek and Badger Mountain, respectively. Although the model underestimates habitat quality, it may be useful in predicting habitat factors which limit deer herd productivity. Duck Creek deer productivity was found to be limited by availability of energy, and Badger Mountain productivity was probably limited by phosphorus availability. Inadequacies of the model are discussed.

INTRODUCTION

Of the many extrinsic factors which affect a mule deer (*Odocoileus hemionus*) population and its productivity, one of the most important and the one over which land managers have the most control is the forage component of the habitat (Tueller 1976). Present habitat evaluation techniques, however, do not allow the measurement of the forage resource in a manner which provides a consistent relationship to animal populations and their productivity (Gill 1976, Wallmo, et al. 1977).

Recently, however, several researchers have outlined an approach to evaluate carrying capacity for white-tailed deer (*Odocoileus virginianus*) and mule deer based upon the nutritional requirements of energy and protein (Moen 1973, Robbins 1973, Swift, et al. 1976, Wallmo, et al. 1977, Mautz 1978). Such a nutritional approach includes the measurement of available forage, its quality, and its harvest by the herbivore population, and a comparison of this intake of forage to the animal's requirements. The distinct advantage to such a habitat evaluation approach is its objectivity and the establishment of the direct relationship between a measurable habitat characteristic and the animal population. Such a nutritional "model" would enable a manager to assess such factors as habitat quality and range carrying capacity.

This study was initiated to develop and test a habitat evaluation system focusing primarily upon the forage component of the habitat. If the law of the minimum can be applied to a deer population, then it can be hypothesized that a limiting factor exists, a nutrient in this case, which controls the reproductive output of a deer population. At any point in time (i.e. summer, winter, fall, etc.), fawn production must be less than or equal to the maximum which is possible relative to the most limiting nutrient available. Therefore, if a nutritional model were developed for habitat evaluation, a test of this model could be made by comparing observed fawn production to the predicted (model) fawn production. In the present study, such a model was developed and tested using data collected on two summer deer ranges in Nevada.

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Study Areas

Two study areas were selected in the northern half of Nevada (Figure 1). The Duck Creek Basin study area is located approximately nine miles northeast of Ely, Nevada in White Pine County. The site is characterized predominantly by limestone derived soils, moderate to steep and complex terrain, elevations ranging from 7500 to 9000 feet and a general easterly aspect. The major vegetation associations include small patches of mountain mahogany (*Cercocarpos ledifolius*), juniper (*Juniperus osteosperma*), and communities of mountain brush which include snowberry (*Symphoricarpos rotundifolius*), bitterbrush (*Purshia tridentata*), and sagebrush (*Artemisia tridentata*).

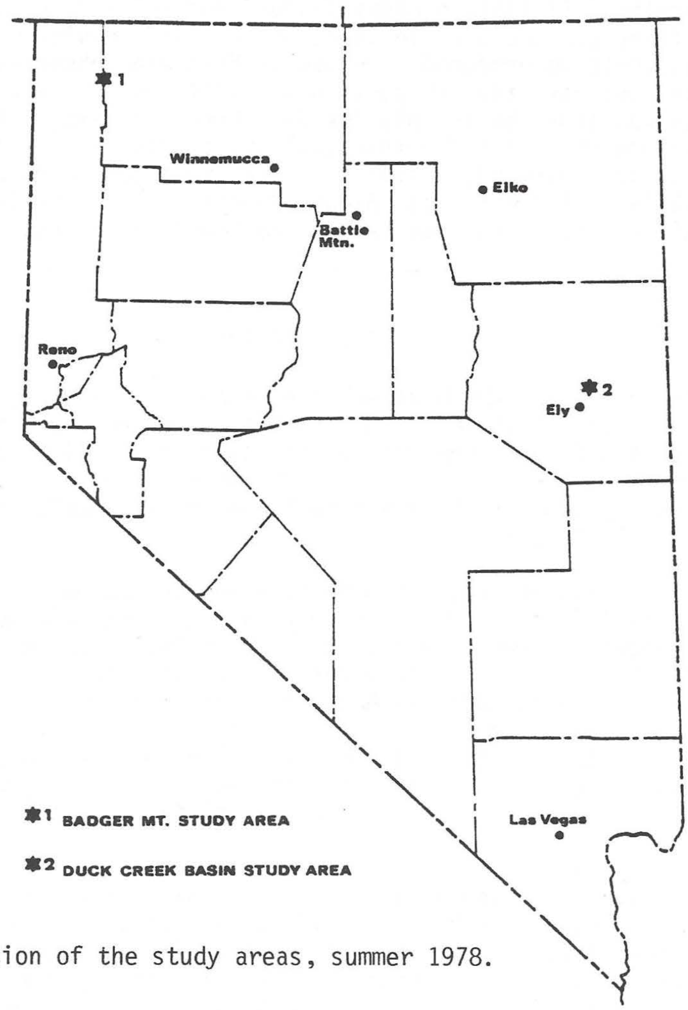

FIGURE 1. Location of the study areas, summer 1978.

The Badger Mountain study area is located on the Sheldon National Antelope Range in northern Washoe County. Soils on this site are generally volcanic in orgin, with moderate to steeply sloping and complex terrain, and elevations which range between 6500 to 7000 feet. The major vegetation communities include extensive stands of mountain mahogany interspersed with communities of big sagebrush and small patches of mountain brush.

The Model

The nutritional model developed is based upon three nutritional components: energy, protein, and phosphorus. Energy and protein are considered important nutrients in the diet of mule deer, and at certain times of the year could become limiting (Dietz and Nagy 1976, Wallmo, et al, 1977). In addition, many western ranges may be defieient in phosphorus, and such deficiencies amy limit the productivity of deer (Dietz and Nagy 1976).

For each nutritional component, the requirements for maintenance, growth, and production must be assessed. In addition, intake rates must be estimated for each based upon the nutrient content of the forage, the digestibility or retention rate of the nutrient, and the forage availability. The following is a brief description of the model parameters developed and a further explanation can be found in Spalinger (1980). All model equations are listed in Table 1, and parameter definitions can be found in Table 2.

Protein

The protein intake of mule deer must be sufficient to offset metabolic losses, to allow for growth to adulthood, and to allow for reproduction. Metabolic losses include those associated with urinary nitrogen loss (UN) and the replacement of sloughed intestinal tract tissues due to food abrasion, termed metabolic fecal nitrogen. The nitrogen loss attributed to UN has been determined by Smith, et al. (1975) to be dependent upon the digestible nitrogen intake (DNI) of the diet, with higher UN losses associated with high DNI levels (Eq. 2, Table 1). At low DNI levels, substantially more nitrogen is recycled as urea through the rumen. Metabolic fecal nitrogen losses are dependent upon the abrasiveness of the forage ingested. Moen (1973) uses a coefficient of abrasiveness to estimate these losses as presented in equation 5.

Since only summer habitat was analyzed in this model, protein requirements for growth and hair replacement may be considered negligible, except for that required by fawns for growth and maintenance.

The protein required by the doe for lactation is based primarily on the quality and amount of milk required by the fawn. The fawn's requirement for milk, however, is dependent upon the stage of rumen development, with an increasing proportion of the intake being attributed to forage intake as the fawn approaches weaning. Moen (1973) estimates the dependency on milk as in equation 6. The daily protein requirement for lactation by the doe can then be calculated as in equations 8 and 9 (Table 1), based upon the fawn's requirement for nitrogen (Qnf), the milk dependence of the fawn (MD), the nitrogen content of milk (Mn), the digestibility of the milk nitrogen (DNm), and the nitrogen costs of milk production.

The protein intake is calculated by estimating the diet composition, the protein content of each component of the diet, and the digestibility of the forage protein. Digestibility of the forage protein was found by Robbins (1973) to be proportional to its protein content which he estimated by equation 12 (Table 1).

Energy

The energy requirements were calculated using the equations 13-25 presented in Table 1. Energy demands included those of maintenance, activity (standing, foraging, walking, running), growth (fawns), and milk production.

When considering energy costs, several habitat components can be assessed and their effect upon deer can be determined. In this respect, the model developed assesses the effect of water distribution and forage availability on deer energy expenditures.

TABLE 1. A summary of the formulae utilized in the nutritional model developed for mule deer.

EQUATION NUMBER	MODEL PARAMETER	EQUATION	SOURCE
1	Dry Matter Intake	$DMI = e^{(4.87344 + 3.66233 \ln DE - 1.64367 DE)}$	Ammann et al. 1973, Alldredge et al. 1974, Wallmo et al. 1977
2	Urinary Nitrogen	$Qeun = 1.035 - 1.021 DNI + 0.480 DNI^2$	Smith et al. 1975
3	Urinary Protein	$Peun = 6.25 Qeun$	
4	Metabolic Fecal Nitrogen	$Qmfn = 7.55 DMI$	Robbins et al. 1974
5	Metabolic Fecal Protein	$Pmfn = 6.25 Qmfn$	
6	Rumen Development	$MD = 113.6 - 4.5 W_{kg}$	Moen 1973
7	Gestation Nitrogen	$Ng = e^{(0.0275 t_d - 3.3856)}$	Robbins and Moen 1975
8	Milk Production	$Qmp = (Qnf)(MD)(Mn)(DNm)$	Moen 1973
9	Milk Production	$Qmp = W_{kg}^{.75} (MD)(203.88)$	Moen 1973, Silver 1961, Smith et al. 1975
10	Protein Lactation	$Pl = .155 Qmp$	Moen 1973
11	Total Protein	$P_T = Peun + Pmfn + Pl$	
12	Dig. Protein Intake	$DPI = 95.7 (Qpro) - 4.883$	Robbins 1973
13	Maintenance Energy	$Qm = 70 W_{kg}^{.75}$	Moen 1973
14	Metabolizable Energy	$ME = .83 DE$	Ullrey et al. 1969,1970, Wallmo et al. 1977
15	Standing Energy	$Qes = 11.79 W_{kg}^{.75} (FTSD)$	Moen 1973
16	Time Spent Standing	$FTSD = (.0934 \sin((jday)(.9863)+77)-.0004)+.100$	Moen 1978
17	Walking Energy	$Qmw = 70 W_{kg}^{.75} + (Ewl)(W_{kg})(V)(24)+(Ewv)(W_{kg})(V)(H)(24)$	Moen 1973
18	Running Energy	$Qer = 560 W_{kg}^{.75} (FTRD)$	Moen 1973
19	Time Spent Running	$FTRD = (-.0006 \sin((jday)(.9863)-103)-.0004)+.006$	Moen 1978
20	Foraging Energy	$Qee = 12.53 W_{kg}^{.75} (FTFD)$	Moen 1973
21	Time Spent Foraging	$FTFD = (.0232 \sin((jday)(.9863)-103)+.0002)+.231$	Moen 1978
22	Gestation Energy	$Qg = e^{(0.2803 + 0.0282 t_d)}$	Robbins and Moen 1975

TABLE 1. Continued......

Equation Number	MODEL PARAMETER	EQUATION	SOURCE
23	Milk Production	$Qmp = (118.5\ W_{kg}^{.75})(2.04 - 0.08\ W_{kg})$	Moen 1973
24	Lactation Energy	$Ql = 1.12\ Qmp$	Moen 1973
25	Total Energy	$Q_T = Qm + Qes + Qmw + Qer + Qee + Ql$	
26	Phosphorus Maint. , Growth	$Pgm = 8.63\ \Delta W_{kg} + .0497\ W_{kg} - 1.50$	ARC 1965
27	Phosphorus Maint.	$Pm = .0497\ W_{kg} - 1.50$	ARC 1965
28	Phosphorus Gestation	$Phr = e^{(1.059 + .00353\ t_d/1.42857)} - 2.88$	ARC 1965, Moen 1973
29	Milk Production	$Qmp = (MD)(.40 + .0497\ W_{kg})/.18$	ARC 1965, Arman et al. 1974
30	Phosphorus Lactation	$Phl = .00362\ Qmp$	
31	Antler Weight	$AWT = e^{(-5.9197 + 3.1892 \log W_{kg})}$	Anderson and Medin 1969
32	Phosphorus in Antlers	$PHA = .08\ AWT$	Banks et al. 1968
33	Phosphorus Antler Growth	$BPHA = .00043\ AWT$	
34	Total Phosphorus	$Ph_T = Pgm + Phl + BPHA$	
35	Foraging Costs	$QMAXF(k) = (W_{kg})(DMI)(.044)/QF$	Spalinger 1980
36	Digestible Energy	$DE = 4.62\ DDM - .158$	Moir 1961

TABLE 2. A summary of the symbols and their definitions utilized in the nutritional model.

Symbol	Definition	Units
DMI	Dry Matter Intake	$g/W_{kg}^{.75}/day$
DE	Digestible Energy Content	Kcal/g
$W_{kg}^{.75}$	Metabolic Body Weight	kg
Quen	Endogenous Urinary Mitrogen	g/day
Puen	Endogenous Urinary Protein	g/day
DNI	Digestible Nitrogen Intake	g/day
Qmfn	Metabolic Fecal Nitrogen	g/day
MD	Rumen Development Coefficient	%
W_{kg}	Body Weight	kg
Pmfn	Metabolic Fecal Protein	g/day
ΔW_{kg}	Weight Gain	kg/day
t_d	Time Elapsed	days
Ng	Nitrogen Required for Gestation	g/day
Qmp	Milk Production Required	g/day
Qnf	Nitrogen Requirement of Fawn	g/day
Mn	Nitrogen Content of Milk	%
DNm	Digestibility of Milk Nitrogen	%
Pl	Protein Required for Lactation	g/day
P_T	Total Protein Required	g/day
Qm	Maintenance Energy Requirement	Kcal/day
ME	Metabolizable Energy	Kcal/g
DE	Digestible Energy	Kcal/g
Qes	Energy Required for Standing	Kcal/day
FTSD	Time Spent Standing	% of day
jday	Day of the Year by the Julian Calendar	
Qmw	Energy Required for Walking	Kcal/day
Ewl	Energy Cost Level of Walking	Kcal/kg/km
Ewv	Energy Cost of Vertical Movement	Kcal/kg/km
V	Velocity	km/hr
H	Vertical Height Ascended	% of V
Qer	Energy Required for Running	Kcal/day
FTRD	Proportion of Day Spent Running	%
Qee	Energy Required for Foraging	Kcal/day
FTFD	Proportion of Day Spent Foraging	%
Qg	Energy Required for Growth	Kcal/day
Qg	Energy Retention of Uterus	Kcal/day
Ql	Energy Required for Lactation	Kcal/day
Q_T	Total Energy Required	Kcal/day
Pgm	Phosphorus, Growth and Maintenance	g/day
Pm	Phosphorus Required for Maintenance	g/day
Phr	Phosphorus Required for Gestation	g/day
Phl	Phosphorus Required for Lactation	g/day
AWT	Antler Weight	kg
PHA	Phosphorus Content of Antlers	g
BPHA	Phosphorus Required for Antlers	g/day
Ph_T	Total Phosphorus Required	g/day
QMAXF(k)	Foraging Cost of Forage k	Kcal/day
QF	Biomass of Forage Available	kg/ha
DDM	Digestible Dry Matter of Forage	%

Water availability was included as an energy cost to deer, assuming that deer must travel to and from the water source at least once each day. This cost was calculated as twice the distance from the center of the study area (the home range of a radio-collared deer) to the water source, times the energy cost of walking. Forage availability was included in a similar manner based upon the assumption that a deer must expend energy in search of food and this energy cost is inversely proportional to the availability of the most limiting forage component of the diet.

Energy intake was calculated by estimating the digestible energy content of the diet and the dry matter intake of the average deer.

Phosphorus

Phosphorus is required by deer for maintenance processes, for growth, and for reproduction and lactation. In addition, adult males require additional phosphorus for antler development. Phosphorus demands are calculated using equations 26-34 presented in Table 1.

Phosphorus intake was calculated similarly to energy intake, by estimating the phosphorus content and digestibility of the diet. Due to lack of data, phosphorus digestibility was assumed to be proportional to dry matter digestibility.

Intake Rates

Ideally, any nutrient demand can be satisfied if the intake of forage is large enough. However, the intake rate of mule deer is limited, primarily due to rumen size and turnover rates. Turnover rates, in turn, are primarily determined by the digestibility of the forage consumed (Blaxter, et al. 1961. Balch and Campling 1962, Campling 1964, Conrad, et al. 1964, Ammann, et al. 1973), although other factors have been implicated as well (McEwen, et al. 1957, Balch and Campling 1962, Conrad, et al. 1964, Conrad 1966, Field 1966, Ozoga and Verme 1970, Milchunas, et al. 1978). Based upon the work of Ammann, et al. (1973), Alldredge, et al. (1974), and Wallmo, et al. (1977), a forage intake model was developed (Figure 2) to estimate forage intake rates of mule deer based primarily upon forage digestibility. Although Figure 2 indicates that intake will decline rapidly on diets with a higher digestibility than 2.2 Kcal/g, this energy level corresponds to a forage digestibility level greater than 50 percent, which is normally encountered only in spring and summer diets. Deer may indeed limit intake rates due to thermal imbalances which may occur in the summer when consuming diets of higher energy content than 2.2 Kcal/g (Short 1975).

METHODS

The data required to test the model included the determination of forage availability, food habits of deer, protein, phosphorus, and idgestibility of the forages present, water distribution, and fawn production. For each study area, the approximate home range of at least one radio-collared animal was determined in cooperation with the Nevada Department of Wildlife on Duck Creek (Stiver 1978), and in cooperation with the University of Nevada deer studies on Badger Mountain.

The vegetative types were delineated on each home range area and each was sampled using a double sampling weight estimate technique (Pechanec and Pickford 1937, Wilm, et al. 1944). In total, 28 transects of 10 estimated and 3 clipped .89 m^2 (9.6 $ft.^2$) plots were established in 12 habitat types (69.2 hectares) on Duck Creek and 33 transects were established n 11 habitat types (174.3 hectares) on Badger Mountain. Forage was considered available if: 1) Forage was under 152 cm (5 ft.) in height. 2) For shrubs, only current year leaders were considered. 3) Forbs and grasses were not unreachable by deer due to shrub cover.

Samples of all forages were returned to the lab for standard dry matter determinations, phosphorus, and protein analysis (AOAC 1970). Digestible dry matter and thus digestible energy content of each species was determined in duplicate using cow inocula in an in-vitro digestion trial (Goering and Van Soest 1970).

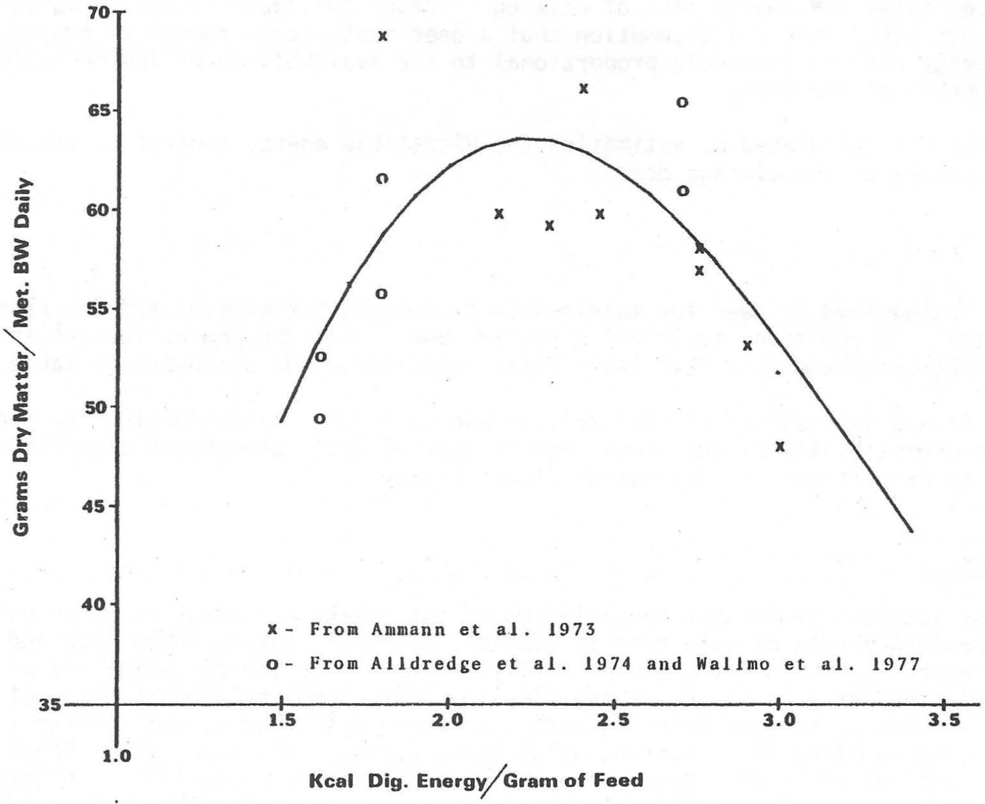

FIGURE 2. The relationship between dry matter intake (DMI) and digestible energy content of the forage. $\mathrm{DMI} = e^{(4.87344 + 3.66233 \ln \mathrm{DE} - 1.64367\ \mathrm{DE})}$, Where DMI is the dry matter intake in $\mathrm{g}/W_{kg}^{.75}$/day and DE is the digestible energy of the forage in Kcal/g (data form Ammann et al. 1973, Alldredge et al. 1974, and Wallmo et al. 1977).

Food habits were estimated by fecal analysis (Hansen, et al. 1977) from a fecal sample of two pellets from at least 15 fresh pellet groups. One sample was collected from the approximate center of each of the two study areas.

Estimates of fawn production were obtained from Nevada Department of Wildlife helicopter surveys which are conducted in the fall on a yearly basis.

Water distribution was determined by mapping all water sources on aerial photographs and determining the average distance from these sources to the center of the study area.

RESULTS

The Duck Creek study area was a relatively productive deer range, with an average dry weight standing biomass of 545 kg/hectare. Of this, more than 12 species of grasses contributed 25% of the forage available, more than 40 forbs contributed about 26% of the forage, and 12 shrubs and trees contributed approximately 50%.

Major species available included bluebunch wheatgrass (*Agropyron spicatum*), Great Basin wildrye (*Elymus cinereus*), Columbia needlegrass (*Stipa columbiana*), arrowleaf balsamroot

(*Balsamorhiza sagittata*), tapertip hawksbeard (*Crepis acumenata*), lupine (*Lupinus* sp.), beardtongue (*Penstemon* sp.) sagebrushes, green rabbitbrush (*Chrysothamnus viscidiflorus*), juniper, bitterbrush, and snowberry (Table 3).

Deer food habits according to fecal analysis included approximately 12% grasses, with bluebunch wheatgrass being the most prevalent, approximately 8% forbs, with longleaf phlox (*Phlox longifolia*) being the most common, and 80% shrubs, with snowberry being the most prevalent, followed by bitterbrush and then sagebrush (Table 3).

Badger Mountain was much less productive than the Duck Creek area, with an average estimated dry weight standing biomass of 234 kg/ha. Of this, 23% were grasses, dominated by Idaho fescue (*Festuca idahoensis*) and bottlebrush squirreltail (*Sitanion hystrix*), 23% were forbs dominated by arrowleaf balsamroot, Rocky Mountain iris (*Iris missouriensis*), and wooley groundsel (*Senecio canus*), and 54% were shrubs and trees dominated by big sagebrush, bitterbrush, and green rabbitbrush. Although mountain mohogany was a major cover type of the area, covering over 40% of the study area, most was unavailable to deer, and only contributed 1% to the forage available (Table 4).

Deer food habits at Badger Mountain included 1% grasses, 6% forbs dominated by arrowleaf balsamroot and Hood's phlox (*Phlox hoodii*), and 93% shrubs dominated by bitterbrush, followed by mountain mohogany, sagebrush, and snowberry (Table 4).

Model Results

Based upon the information collected, the nutritional model was utilized to predict the fawn production for these two ranges, and the results were compared to observed fawn production. Tables 5 and 6 present typical model results when nutritional status is in balance (intake = requirements).

For the average Duck Creek doe, dry matter intake is approximately 63 $g/w^{.75}$/day or 1.5 kg/day for a 66 kg doe. At this intake rate, digestible protein intake is approximately 137 g/day, metabolizable energy intake is 3014 Kcal/day and digestible phosphorus intake is estimated at 3.0 g/day. At this intake rate, only 50 fawns per 100 does could be produced before energy became a limiting factor. Production greater than this rate is estimated to require loss of weight by the doe to support the added stress of lactation.

The observed Duck Creek fawn production was estimated to be approximately 97 fawns per 100 does in 1978, or approximately 194% of the calculated production rate. At this rate, the model predicted that both protein and energy would be deficient in the diet (Table 7).

Badger Mountain deer nutrient intakes were similar to Duck Creek intake rates (Table 6) with minor differences occurring due to diet composition and quality. Fawn production was predicted to be very low, at 10 fawns per 100 does, with the limiting nutrient being phosphorus. The observed fawn production was estimated at 57 fawns per 100 does which is approximately 570% greater than calculated. At the observed fawn production, the limiting nutrient was still predicted to be phosphorus with both energy and protein being in a positive status (Table 7).

DISCUSSION

Obviously there are problems with the present model which preclude its application to habitat management at the present time. One of the principal objectives, however, of ecological modeling is to guide the researcher in identifying areas of technical inadequacy in order to improve future studies, understanding, and application. In the analysis of model parameters and results, several problems were identified which could cause the model to underestimate actual conditions. Future application of habitat modeling depends upon increasing our understanding of several topics including:

1. Digestibility/intake relationships
2. Phosphorus requirements
3. Forage selection and diet analysis

TABLE 3. Average forage biomass and composition and diet composition of mule deer for Duck Creek study area, June, 1978.

Species	Forage Base		Diet
	Ave. Biomass[1] (Kg/ha)	Species Composition	(%)
Agropytron smithii	1.3	.2	
A. spicatum	69.0	12.7	5.8
Bromus marginatus	.2	.04	.4
B. tectorum	9.5	1.7	
Carex spp.	2.5	.5	.5
Elymus cinereus	21.2	3.9	
Festuca idahoensis	5.0	.9	.5
Melica bulbosa	.3	.1	tr
Orygopsis hymenoides	3.1	.6	.2
Poa sanbergii	9.5	1.7	
Situanion hystrix	3.6	.7	1.9
Stipa columbiana	13.1	2.4	1.8
Unknown grasses			.8
TOTAL GRASSES	138.3	25.4	11.9
Aster scopulorum	2.8	.5	tr
Astragalus lentiginosus	3.7	.7	.1
A. purshii	1.8	.3	
Balsamorhiza sagittata	14.7	2.7	.2
Berberis repens	1.6	.3	
Calochortus spp.	.04	.01	
Castelleja spp.	.3	.1	
Cirsium spp.	.8	.1	
Collinsia parviflora	.4	.1	
Crepis acuminata	9.4	1.7	
Cryptantha affinis	.8	.1	
C. flavoculata	3.1	.6	
Erigeron pumilus	2.3	.4	
Erigeron spp.	.9	.2	.8
Eriogonum caespitosum	2.4	.4	
E. microthecum	2.1	.4	
E. umbellatum	2.5	.5	.4
Geum ciliatum	1.0	.2	
Haplopappus acaulis	2.1	.4	
Comandra pallida	.7	.1	
Lappula spp.	.7	.1	
Linum lesiwii	.2	.04	
Lethospermum ruderale	.3	.1	.1
Lupinus spp.	45.3	8.3	.2
Lygodesmia spinosa	4.5	.8	
Mertensia oblongifolia	1.5	.3	tr
Microseris nutans	2.8	.5	
Myosotis spp.	1.8	.3	.4
Oenothera caespitosa	.04	.01	
Opuntia spp.	7.6	1.4	
Penstemon gracilentus	.01	.01	
P. speciosus	9.0	1.7	
Penstemon spp.	3.6	.7	
Phloyx longifolia	8.4	1.5	1.1
Polygonum douglasii	1.2	.2	
Pontentilla glandulosa	.02	.01	.4
Senecio multilobatus	1.6	.3	
Taraxacum officinale	.03	.01	
Viola spp.	.6	.1	.1
Other forbs			3.6
TOTAL FORBS	142.6	26.2	7.5
Aretemisia arbuscula	26.6	4.9	
A. tridentata	30.2	5.5	17.8
Chrysothamnus nauseosus	.4	.1	1.1
C. viscidiflorus	17.2	3.2	
Juniperus osteosperma	111.1	20.4	.2
Pinus monophylla	1.7	.3	
Prunus virginiana	.5	.1	.1
Purshia tridentata	51.5	9.5	21.5
Rosa woodsii	.8	.1	
Salix spp.	.6	.1	
Sumphoricarpos rotundifolius	19.7	3.6	39.0
Tetradymia canescens	3.6	.7	
Other shrubs			.6
TOTAL SHRUBS	263.9	48.4	80.3
TOTAL BIOMASS	544.8		

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[1] dry weight

TABLE 4. Average forage biomass and composition, and diet composition of the mule deer for Badger Mountain study area, July, 1978.

Species	Forage Base		
	Ave. Biomass[1] (Kg/ha)	% Species Composition	Diet (%)
Agropyron spicatum	1.9	.8	.3
Carex spp.	4.8	2.1	
Elymus cinereus	.1	.04	
Festuca idahoensis	11.9	5.1	
Juncus	.2	.1	
Poa ampla	.3	.1	
P. sandbergii	1.5	.6	
Sitanion hystrix	11.1	4.7	.3
Stipa californica	9.6	4.1	
S. columbiana	6.4	2.7	
S. comata	.3	.1	
S. thurberiana	4.5	1.9	
Other grasses			.5
TOTAL GRASSES	52.5	22.5	1.1
Achillea lanulosa	.2	.1	
Agastache agricifolia	1.3	.6	
Agoseris clauca	1.7	.7	tr
Antennaria rosea	.4	.2	
Arabis sp.	.6	.3	
Astragalus purschii	.2	.1	
Balsamorhiza sagittata	13.7	5.9	1.4
Castilleja sp.	.3	.1	
Cirsium sp.	.2	.1	
Collomia linearis	.2	.1	
Crepis acuminata	1.7	.7	
Erigeron filifolius	.9	.4	.5
Eriogonum umbellatum	.8	.3	
Eupatorium occidentale	.5	.2	
Frasera albicaulis	.5	.2	
Iris missouriensis	7.2	3.1	
Leptodactylon pungens	.3	.1	
Lomatium canbyi	.8	.3	
Lupinus caudatus	15.8	6.8	.7
Mertensia oblongifolia	.3	.1	.3
Monardella odoratissima	.2	.1	
Penstemon sp.	.2	.1	
Phacelia hastata	.9	.4	.5
P. humilis	.2	.1	
Phlox hoodii	1.8	.8	1.0
Phoenicaulis cheiranthoides	.2	.1	.8
Polygonum douglasii	.7	.3	
Senecio canus	2.7	1.2	
Taraxacum officinale	.2	.1	
Other forbs			1.2
TOTAL FORBS	54.7	23.3	6.4
Artemisia arbuscula	.4	.2	
A. ludoviciana	.1	.04	
A. tridentata	91.5	39.1	2.9
Cercocarpus ledifolius	2.7	1.2	10.7
Chrysothamnus nauseous	.7	.3	
C. viscidiflorus	7.7	3.3	
Holodiscus discolor	.6	.3	.3
Populus tremuloides	.4	.2	
Purshia tridentata	18.5	7.9	76.6
Ribes velytium	.9	.4	.3
Symphoricarpos longiflorus	2.1	.9	1.7
Tetradymia glabrata	1.3	.6	
TOTAL SHRUBS	126.9	54.3	92.5
TOTAL FORAGE BIOMASS	233.9		

[1] dry weight

TABLE 5. Estimated nutritional requirements, intakes, and status of mule deer at Duck Creek, June 1978.

PRODUCTION (FAWNS/DOE) = .50; FAWN GROWTH RATE = .10 Kg/day.

ANIMAL REQUIREMENTS (AVE. DAILY, AVE. MAX. DAILY)

NUTRIENT DEMAND	BUCK		DOE		AVE. DEER	
	AVE	MAX	AVE	MAX	AVE	MAX
Protein, Total	72.20 [1]		86.87	89.94	83.57	85.95
Protein, EUN	3.88		3.08		3.08	
Protein, MFN	69.12		62.68		64.13	
Protein, Lactation			21.12	24.18	16.37	18.75
Energy, Total	2893.71 [2]		3036.18	3071.60	3004.15	3031.61
Energy, Maint.	1624.58		1473.09		1507.15	
Energy, Standing	15.04		13.64		13.96	
Energy, Foraging	125.12		113.46		116.08	
Energy, Walking	998.99		806.92		850.10	
Energy, Running	129.97		117.85		120.57	
Energy, Lactation			511.22	546.64	396.30	423.75
Phos, Total	2.531 [3]		1.014	1.388	1.355	1.645
Phos., Maint.	1.790		1.388		1.478	
Phos., Antler Gr.	.741				.167	
Phos., Lactation			-.373	0.000	-.290	0.000

NUTRIENT INTAKE RATES (AVE INTAKE/DAY)

NUTRIENT	BUCK	DOE	AVE. DEER
Dig. Protein	151.47	137.35	140.53
Maint. Energy	3324.15	3014.18	3083.86
Dig. Phosphorus	3.342	3.031	3.101
Dry Matter	63.12 [4]	63.12	63.12

NUTRITIONAL STATUS

NUTRIENT	BUCK	DOE	AVE. DEER
Protein	79.28	50.48	56.95
Energy	430.438	-22.007	79.705
Phosphorus	.811	2.016	1.746

[1] g/day
[2] KCal/day
[3] g/day
[4] g/Kg BW$^{.75}$/day

Ruminant digestion and intake are complex processes involving the rumen microbiota, forage characteristics and physiological interactions between protein and energy supplies. A rumen microflora which is adapted to a specific forage regime is more efficient at digestion than one which is not (Nagy and Tengerdy 1968). Consequently, digestibility data determined in-vitro using livestock rumen inocula may not adequately assess actual forage quality for mule deer. Forage intake may also be significantly affected by other factors not assessed using the present model. Such factors as lignin content (Milchunas, et al. 1978), the associative effects between protein and energy levels of forages (Robbins 1973, Milchunas, et al. 1978), and the effects of the animal's physiological state (i.e. lactation effects) (McEwen, et al. 1957, Balch and Campling 1964, Conrad, et al. 1964, Conrad 1966, Field 1966, Ozoga and Verme 1970) are not addressed, and may significantly affect model performance.

Phosphorus assessment by the model may also be in error. Phosphorus can probably be mobilized by the doe during peak periods of lactation, if sufficient phosphorus is stored in bone marrow and other areas of the body. On Badger Mountain, it can be hypothesized that

TABLE 6. Estimated nutritional requirements, intakes and status of mule deer at Badger Mtn., July 1978.

PRODUCTION (FAWNS/DOE) = .10; FAWN GROWTH RATE = .10 Kg/day.

ANIMAL REQUIREMENTS (AVE. DAILY, AVE. MAX. DAILY)

NUTRIENT DEMAND	BUCK AVE	BUCK MAX	DOE AVE	DOE MAX	AVE. DEER AVE	AVE. DEER MAX
Protein, Total	72.25[1]		70.05	70.68	70.56	71.04
Protein, EUN	3.13		3.13		3.13	
Protein, MFN	69.12		62.68		64.16	
Protein, Lactation			4.24	4.87	3.27	3.75
Energy, Total	2346.43[2]		2202.69	2209.71	2235.86	2241.26
Energy, Maint.	1624.58		1473.09		1508.05	
Energy, Standing	14.91		13.52		13.84	
Energy, Foraging	125.76.		114.03		116.74	
Energy, Walking	451.21		381.72		397.76	
Energy, Running	129.97		117.85		120.64	
Energy, Lactation			102.48	109.50	78.83	84.23
Phos, Total	2.531[3]		1.313	1.388	1.594	1.651
Phos., Maint.	1.790		1.388		1.480	
Phos., Antler Gr.	.741				.171	
Phos., Lactation			-.074	0.000	-.057	0.000

NUTRIENT INTAKE RATES (AVE INTAKE/DAY)

NUTRIENT	BUCK	DOE	AVE. DEER
Dig. Protein	134.76	122.19	125.09
Maint. Energy	3644.51	3304.67	3383.09
Dig. Phosphorus	1.375	1.247	1.276
Dry Matter	63.12[4]	63.12	63.12

NUTRITIONAL STATUS

NUTRIENT	BUCK	DOE	AVE. DEER
Protein	62.51	52.14	54.53
Energy	1298.883	1101.975	1147.231
Phosphorus	-1.156	-.067	-.318

1 g/day
2 KCal/day
3 g/day
4 $g/KgBW^{.75}/day$

TABLE 7. The predicted and observed fawn production rates on Duck Creek and Badger Mountain and their associated nutrient status.

Range	Model	Fawn Production (per 100 does)	Nutrient Status		
			Protein	Energy	Phosphorus
Duck Creek	Observed	97	-	-	+
	Predicted	50	+	0	+
Badger Mountain	Observed	57	+	+	-
	Predicted	10	+	+	0

most deer are not able to breed on a yearly basis, but must utilize alternate years to store phosphorus and other nutrients in preparation for the coming breeding season (Mansell 1974, Belovsky 1978). This would explain why Badger Mountain fawn production has consistently been observed between 50 and 80 fawns per 100 does during the last three years. Future models must, however, be based upon better knowledge of the phosphorus requirements of mule deer for maintenance and reproduction.

A third likely source of error in the model results is the inaccurate determination of the diet using fecal analysis. Many studies have shown that highly digestible forages such as forbs are not accurately represented in the diet when using fecal analysis (Jacobs 1973, Anthony and Smith 1974, McInnis 1976, Pulliam 1978, Vavra, et al. 1978). Grasses and shrubs being more highly cutinized pass through the digestive system leaving many more recognizable fragments in the feces. Consequently, forbs and other species which are less cutinized are underestimated considerably in the diet, and shrubs and grasses are overestimated when using this technique. The model would, therefore, likely underestimate the correct nutritional value of the animal's diet.

CONCLUSION

Two of the principle objectives of ecological modeling are to develop the ability to predict ecological processes, and to guide the researcher in identifying areas of technical inadequacy. In this respect, the nutritional model developed here has at least partially succeeded. While identifying several critical animal/habitat relationships which apparently will require further research effort, the model also provides new insight into the habitat factors which may be limiting mule deer productivity on the two areas studied.

Because the model has the ability to quantitatively assess forage availability and forage quality in terms of digestible energy, protein, and phosphorus, and compare these factors to mule deer physiological needs, it is able to predict in a relative manner the limiting habitat factors imposed upon mule deer. This analytic ability has not been available until now.

The model indicates that Duck Creek deer may be producing below their physiological capability due to inadequate energy supplies, while Badger Mountain deer are possibly limited by phosphorus availability.

The model also indicates that, based upon nutritional factors only, Duck Creek habitat is capable of producing 55 to 80 percent more mule deer than Badger Mountain habitat. Because observed fawn production was only 41 percent higher on Duck Creek than on Badger, it becomes obvious that the model requires modification or refinement or that other unidentified limiting factors may be present.

The habitat model presented here also pinpoints the needs for additional research into such subjects as animal nutritional requirements, forage selection and dietary analysis, and forage intake/digestion processes.

The result of future endeavors into such problems and applications may well be a base of knowledge which would enable biologists and land managers to assess habitat quality, forage requirements, forage selection, limiting habitat factors, carrying capacities, animal productivity, and possibly many other animal/habitat relationships.

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