Predicting White-tailed Deer Carrying Capacity Using Grazeable Biomass and Tame Deer

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Abstract: Density-dependent population models likely are inappropriate for white-tailed deer (*Odocoileus virginianus texanus*) in southern Texas due to variable precipitation. We used a tame-deer technique to estimate carrying capacity and correlated results with precipitation and forage biomass. Carrying capacity estimates using digestible energy (DE) consumed by 12 deer were determined using 2 treatments (supplemented and non-supplemented) during 7 trials. Deer were placed in 14 0.33-ha randomly-located enclosures between May 1990 and May 1991. Mean estimates were 0.62 deer/ha/year (SE = 0.27) for non-supplemented enclosures and 1.00 deer/ha/year (SE = 0.57) for supplemented enclosures. Low estimates occurred during summer and high estimates occurred during spring. Precipitation (cm) and forage biomass (kg/ha) were estimated for each trial. Correlations ($P < 0.05$) were positive between carrying capacity estimates and live biomass, forbs, grass, and precipitation, and negative between carrying capacity and dead biomass for the supplemented enclosures. Multiple regression analysis indicated that dead biomass and precipitation were the most significant variables for use in a predictive model. The tame-deer technique for estimating carrying capacity may be useful for determining environmentally stressful periods and aiding decision-making in population management of large herbivores.

Proc. Annu. Conf. Southeast. Assoc. Fish and Wildl. Agencies 51:238–249

Population management is effective only if major processes that influence populations are understood. Population biologists have proposed simple models to explain large mammal population dynamics and discussed requirements for testing them (Caughley 1976, Eberhardt 1988). McCullough (1979) successfully adapted a stock recruitment model to an enclosed white-tailed deer population on the George

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Reserve in Michigan. Stock recruitment models are based upon density-dependent mortality and recruitment in populations with a stable carrying capacity.

It is unlikely that density-dependent models are appropriate for populations of white-tailed deer in southern Texas. Density-dependent processes likely are overwhelmed by frequently-changing carrying capacity caused by variable precipitation and its effects on primary productivity. Average annual precipitation in southern Texas is 64 cm with a coefficient of variation of 35% (Norwine and Bingham 1985). Thus, a population may be significantly below carrying capacity in a wet year and above carrying capacity in a succeeding drought year, complicating the use of density-dependent models. McCullough et al. (1990) reported that frequent, large-magnitude changes in the environment caused density-independent changes in the deer population. Shea et al. (1992) reported deer populations in Florida to be density-independent in areas where forage is abundant but of poor quality, causing a low level of competition between deer even at relatively high densities. We propose that deer populations in southern Texas can be modeled using vegetation dynamics, which are a direct function of precipitation. Whereas density-dependent responses drive stock recruitment models, vegetative biomass would drive a simple model explaining dynamics of southern Texas deer populations.

Traditionally, carrying capacity has been determined by measuring the amount of available forage and then measuring the amount of forage utilized. More recently, carrying capacity estimates have been determined using supplies of available forage dry matter and energy (Mautz 1978) and nitrogen (Hobbs and Swift 1985). Carrying capacity estimates based on estimated digestible energy (DE) consumed by tame white-tailed deer are an alternative. The tame-deer technique was first used with white-tailed deer in Pennsylvania (Clark 1977, Potts and Cowan 1983, Drake and Palmer 1986) and more recently in southern Texas (McCall 1988, McCall et al. 1997). This technique uses change in body mass by tame deer in field enclosures to estimate digestible energy available for deer consumption. The energy estimate is converted to carrying capacity by dividing by daily energy requirements of deer.

The tame-deer technique may be less biased and more accurate than forage-based techniques because deer themselves are used to estimate carrying capacity (Clark 1977, McCall 1988). Errors associated with determining which parts of the plant to sample are avoided and plots, counts, and vegetative measurements are unnecessary (Clark 1977). Further, while vegetation surveys measure quantity of forage present and utilized, the tame-deer technique measures value of that forage to deer.

Assumptions related to the tame-deer technique include: (1) a regression equation accurately predicts DE consumed by deer, (2) feeding behavior of wild and tame deer is similar (Bartmann 1982, Olson-Rutz and Urness 1987), (3) study deer integrate impinging factors into a broad response that was reflected in mass change, and (4) rate of mass change among individual deer is independent of body size. Our objectives were to determine instantaneous carrying capacity of a white-tailed deer habitat in southern Texas using enclosures and to determine if grazeable biomass could be used to predict instantaneous carrying capacity.

We thank D. L. Drawe, J. Cox, B. Martinez, D. Smith, E. Schulz, and B. Dekker for their field assistance. Special thanks go to L. Landry, Y. Ballard, and B. Trant. Financial support was provided by the Rob and Bessie Welder Wildlife Foundation and the Caesar Kleberg Wildlife Research Institute. We thank D. L. Drawe, E. C. Hellgren, R. Bingham, D. Hewitt, and R. L. Marchinton for reviewing the manuscript and providing technical assistance in their areas of expertise. This is Welder Wildlife Foundation Contribution No. 505.

Methods

Study Area

Research was conducted on an 807-ha area of the 3,158-ha Welder Wildlife Refuge, San Patricio County, Texas. The refuge lies within the transition zone between the Gulf Prairies and Marshes and the South Texas Plains (Gould 1969). The climate ranged from humid subtropical to subhumid with annual maximum and minimum temperatures of 36 and 8 C (Guckian and Garcia 1979). Average annual precipitation was 88.9 cm with peaks in late spring and early fall. Predominant woody vegetation on the Victoria clay soil was honey mesquite (*Prosopis glandulosa*), blackbrush (*Acacia acacia*), huisache (*A. smallii*), twisted acacia (*A. tortuosa*), and agarito (*Berberis trifoliolata*; Drawe et al. 1978). Vegetation on the refuge was described in detail by Box and Chamrad (1966) and Drawe et al. (1978).

Twenty-four enclosure sites were randomly selected within the study area. Two portable, deer-proof field enclosures, constructed from 2.13-m high Tensar Polygrid ranch fence, were located at 2 of the 24 enclosure sites bimonthly. Each 0.33-ha field enclosure was divided through the center by fencing, creating 2 0.167-ha treatment enclosures. Enclosure size, although adjustable, was chosen for logistical reasons, to assure sufficient forage for trials (Potts and Cowan 1983, McCall 1988), and was based on enclosure sizes from a similar study in Texas (McCall 1988). Prior to erecting enclosures, we mowed a swath around the perimeter to facilitate fence construction. Following completion of each trial, enclosures were dismantled, transported to the next 2 sites, and reconstructed.

Deer Mass Measurements

Adult female deer ($N = 12$), estimated to be ≥ 4.0 years of age, were paired by body mass and a member of each pair randomly assigned to 1 of 2 treatment groups each trial. One treatment group (non-supplementally-fed) consisted of 6 deer that had access only to natural forage within their half of the enclosures. The other group (supplementally-fed) of 6 deer was treated similarly, except a complete pelleted feed was provided *ad libitum* in their halves of the enclosures (3 deer on half of each of the 2 enclosures received supplemental feed, while the remaining 3 deer on the opposite half of the same enclosures did not receive supplemental feed). This second treatment was incorporated for comparison purposes and to estimate maximum performance under the stress of the pen conditions utilized in this study. In addition, Drake and Palmer (1986) suggested providing supplemental feed to assure that deer lose mass at a moderate rate. Supplemental feed was guaranteed to contain a minimum of 16% crude protein, 2.5% crude fat, 0.6% phosphorus, and maximum 14% crude fiber. Feed was weighed to the nearest 0.1 kg daily to measure consumption. Water was available *ad libitum* for both treatment groups throughout each trial.

Approximately bimonthly, deer were transported in 2 groups of 6 from a 0.8-ha holding pen located near refuge headquarters to the field enclosures. All feed was removed 24 hours prior to transport to standardize rumen fill (Potts and Cowan 1983) and to assure that deer would be more cooperative. The first group of 6 deer were transported (5–10 km) to the first enclosure site, weighed individually in a holding crate positioned on a Micropower 2000™ portable platform scale (Waterford Corp., Fort Collins, Colo.) to the nearest 0.1 kg., and then released into their respective halves of the enclosure. The remaining 6 deer were transported to the second site where the weighing process was repeated.

Approximately every week thereafter, all deer were reweighed to monitor change in mass and to assess condition. Trials were terminated, to avoid unduly stressing deer, when ≥1 deer experienced a decrease in mass of ≥1.5 kg between weighings. Mass loss normally occurs at <1 kg per week (Clark 1977). All deer were transported back to the holding pen until enclosures could be dismantled, moved to 2 new sites, and reconstructed. To monitor transportation effects on the deer, 5–6 deer were weighed at the holding pen before being forced into the trailer, then reweighed immediately after transport to the enclosure site. When trials were not being conducted, all deer were kept in the holding pen and fed a complete pelleted ration *ad libitum.*

During trials 1 and 7, deer were in their third trimester of gestation. All deer that gave birth to fawns while in enclosures were reweighed as soon as possible after parturition. Mass (kg) immediately after parturition was used as the initial mass for calculations of carrying capacities. All fawns were removed from females 2–5 days after birth to reduce effects of physiological stress caused by lactation.

Biomass Determination

To determine if biomass measurements were correlated with deer performance and estimated carrying capacities, grazeable plant biomass was estimated bimonthly at 150 of 480 sites within the 24 enclosure sites. Sampling design was systematically random, with 10 sampling sites chosen at random distances perpendicular to transect lines through the center of each enclosure half. At each sampling site, a 0.25-m^2 rectangular frame was used and all herbaceous vegetation with its base within the frame was sampled (Gysel and Lyon 1980). Along with herbaceous material, leaves from grazeable portions of shrubs were clipped to 1.5-m high, the approximate reach of a feeding deer. Clipped vegetation was sorted into browse, grasses, and forbs. Each group was further divided into live and dead components. Sorted vegetation was placed into a forced-air drier and dried for 24–48 hours at 50 C. The air-dried, sorted vegetation was weighed to the nearest 0.1g.

Data Analyses

The regression equation derived by Drake and Palmer (1986) was used to predict DE intake for the study deer. Their regression equation was:

$$Y = 0.0844X - 13.4.$$

where:

Y = rate of mass change (g/kg$^{0.75}$/day)
X = predicted intake (kcal/kg$^{0.75}$/day)

and was based on results of research conducted by Clark (unpubl. data, Pa. State Univ.) on 19 female deer in Pennsylvania during 2 successive winters. Clark (unpubl. data, Pa. State Univ.) fed deer different levels of digestible energy and determined rates of mass loss. He also confined the deer in small enclosures (0.2–15 ha), measured forage intake through bite counts, and periodically weighed the deer to monitor mass loss.

DE consumed/deer during each trial for our study was estimated via a several-step process. We subtracted initial deer mass (kg) from final deer mass (kg) to calculate mass change (kg). Mass change (kg) was converted to grams and divided by trial length (days) to estimate mean mass change (g/day). We converted the average of the initial and final deer mass (kg) to average metabolic mass (kg$^{0.75}$). We estimated rate of mass change (Y, g/kg$^{0.75}$/day) by dividing mean mass change (g/day) by average metabolic mass (kg$^{0.75}$). Estimated rate of mass change (Y, g/kg$^{0.75}$/day) was used in Drake and Palmer's (1986) regression equation to estimate predicted intake (X, kcal/kg$^{0.75}$/day). Finally, digestible energy intake (kcal) was estimated by multiplying predicted intake (X, kcal/kg$^{0.75}$/day) by average metabolic mass (kg$^{0.75}$) and trial length (days). When this product resulted in a negative value, the value was replaced by 0.0. Negative values occurred when deer lost mass rapidly ($\geq$1.5 kg per week) and were the result of a predictive equation that was linear when the actual relationship was likely curvilinear at low intake levels. Total digestible energy intake per treatment enclosure (kcal) was estimated by adding digestible energy intake (kcal) for each deer.

Carrying capacity (deer/ha/day) for treatment enclosures was a 3-step process. After dividing total DE (kcal) consumed per treatment enclosure by its area (ha), we divided this quotient (kcal/ha) by the product obtained from multiplying mean average metabolic mass (kg$^{0.75}$/deer) by the deer's estimated daily maintenance requirement (159 kcal/kg$^{0.75}$/day; Clark, unpubl. data, Penn. State Univ.; McCall et al. 1997). Finally, we divided the above value by average trial length (days). McCall et al. (1997) assumed that the regression equation developed by Clark (unpubl. data, Penn. State Univ.) using penned female deer in winter accurately predicted the digestible energy consumed by deer in their study in summer because summer is a period of mass loss for deer in Texas, and winter is a period of mass loss in Pennsylvania. A mean bimonthly carrying capacity was determined for each trial and treatment (supplementally-fed and non-supplementally-fed) by averaging carrying capacities from the 2 enclosures.

A second carrying capacity estimate was determined by dividing carrying capacity (deer/ha/day) by the quotient 365 (days/year) divided by average trial length (days). This second measure was reported as deer/ha/year and was used for comparison with deer density estimates obtained by helicopter census on the study area (Blankenship et al. 1994).

We used Pearson correlation analysis (SAS Inst. 1985) to test for relationships among estimated deer carrying capacities (deer/ha/day and deer/ha/year), biomass (kg/ha) estimates, and precipitation (cm). We used multiple regression analysis (SAS Inst. 1985) to develop predictive models for carrying capacity estimates.

Results

Seven trials were completed between 22 May 1990 and 18 May 1991. Trial length varied from 7 days during trial 2 to 29 days during trial 7 ($\bar{x}$ = 17.9). Precipitation during trials averaged 9.41 cm, 32% below the 35-year mean. Least precipitation occurred during trial 2 (62% below average). Trials 6 and 7 were the only trials with precipitation above the 35-year mean.

Estimated trial carrying capacities varied from 4.4 to 16.3 deer/ha/day ($\bar{x}$ = 12.0, SE = 4.07) for non-supplemented enclosures and from 4.7 to 29.4 for supplemented enclosures ($\bar{x}$ = 19.0, SE = 8.09). The second measure of carrying capacity varied from 0.10 to 0.95 deer/ha/year for non-supplemented enclosures and from 0.10 to 2.06 for supplemented enclosures (Table 1). Biomass (kg/ha) estimates were lowest during trial 6 for all parameters measured except dead biomass. Highest biomass

Table 1. Estimated total digestible energy intake and estimated carrying capacities during 7 foraging trials with tame deer from 22 May 1990 to 18 May 1991 at the Welder Wildlife Refuge, San Patricio County, Texas.

Trial	Dates	Days	N	U/F[a]	Total digestible energyintake (kcal)	Carrying capacity (deer/ha/day)	Carrying capacity (deer/ha/day)
1	22 May-8 Jun	15.5	6	U	229,000	16.3	0.69
		14.4	6	F	373,000	27.0	1.06
2	26 Jun–6 Jul	8.3	5	U	31,800	4.4	0.10
		7.9	6	F	34,600	4.7	0.10
3	2 Aug–22 Aug	18.4	6	U	219,000	14.9	0.75
		18.7	6	F	276,000	17.8	0.91
4	19 Sep–12 Oct	18.5	6	U	168,000	9.9	0.50
		19.0	4	F	302,000	18.5	0.96
5	29 Oct–25 Nov	21.9	6	U	204,000	10.3	0.62
		21.6	4	F	298,000	15.5	0.92
6	23 Jan–14 Feb	18.5	6	U	216,000	13.8	0.70
		17.8	4	F	309,000	20.4	0.99
7	17 Apr–18 May	24.6	6	U	306,000	14.1	0.95
		25.6	6	F	685,000	29.4	2.06

[a] U/F = Treatment (non-supplementally-fed [U] or supplementally-fed [F]).

Table 2. Forage biomass (kg/ha) and precipitation (cm) and correlations with estimated carrying capacities during 7 foraging trials with tame deer from 22 May 1990 to 18 May 1991 at the Welder Wildlife Refuge, San Patricio County, Texas. See Table 1 for dates of the trial.

Trial	Total biomass	Live biomass	Dead biomass	Forbs	Grass	Browse	Precipitation
1	3104	2358	771	1658	241	459	7.04
2	2508	1219	1289	685	225	309	2.98
3	2416	1423	993	760	330	334	7.48
4	2085	1477	608	848	512	118	8.13
5	2150	1488	662	902	469	118	5.47
6	1485	565	919	247	220	98	14.75
7	4622	4218	404	2652	1121	445	20.00
Carrying capacity (deer/ha/day) correlations:							
r(U) =	0.26	0.34	−0.46	0.37	0.16	0.35	0.52
r(F) =	0.55	0.66	0.77[a]	0.68	0.53	0.40	0.72
Carrying capacity (deer/ha/year) correlations:							
r(U) =	0.44	0.55	0.71	0.54	0.55	0.26	0.75[a]
r(F) =	0.68	0.79[a]	−0.87[a]	0.77[a]	0.83[a]	0.33	0.86[a]

a. Significant at the 0.05 level.

estimates occurred during trial 7 for all parameters measured except dead biomass and browse (Table 2).

Significant correlations ($P \leq 0.05$) occurred between carrying capacity (deer/ha/year) estimates for supplemented enclosures, and live biomass, dead biomass, forbs, grass, and precipitation. Correlations for non-supplemented enclosures were significant for only precipitation ($r = 0.75$, $P = 0.05$; Table 2). Correlations between carrying capacity estimates (deer/ha/year) and precipitation (cm) during previous trials were weaker than correlations using precipitation during the trial. Correlations between carrying capacity (deer/ha/year) estimates, biomass (kg/ha) estimates, and precipitation (cm) were stronger for all variables measured (except dead biomass and

Table 3. Multiple regression models ($Y = B_0 + B_2X_1 + B_2X_2 + B_3X_3$) for predicting carrying capacity (deer/ha/year) of white tailed deer from the Welder Wildlife Refuge, San Patricio County, Texas.

Dependent variable (Y)	Independent variables (X_i)	Coefficients (B_i)	R^2	SE	P-value	N
CC-NS[a]	intercept	0.944	0.707	0.550	0.185	7
	precipitation	0.028		0.020	0.250	
	dead biomass (kg/ha)	−0.0006		0.0005	0.306	
	grass (kg/ha)	0.0003		0.0004	0.558	
CC-S[b]	intercept	1.24	0.977	0.259	0.017	7
	dead biomass (kg/ha)	−0.001		0.0002	0.014	
	precipitation (cm)	0.0465		0.011	0.023	
	browse (kg/ha)	0.0008		0.0003	0.089	

a. CC-NS = Carrying capacity (deer/ha/year) for non-supplemented treatment.

b. CC-S = Carrying capacity (deer/ha/year) for supplemental treatment.

precipitation) when all data from trial 2 were deleted. Correlations without trial 2 data were tested because DE (kcal) intake estimates for 7 of 11 deer during the trial were negative and set to 0.0.

Multiple regression analysis showed that the best model (highest R^2 value) for predicting carrying capacity (deer/ha/year) for supplemented enclosures included the variables dead biomass (kg/ha), precipitation (cm), and browse (kg/ha). However, only dead biomass and precipitation were significant ($P \leq 0.05$). No model tested for non-supplemented enclosures included significant variables ($P > 0.05$; Table 3).

Discussion

Correlation analysis suggested that differences in total DE intake estimates and carrying capacity estimates between trials partially were caused by differences in biomass and precipitation. Drake and Palmer (1986) related variable carrying capacity estimates to variable amounts of available native forage. Deer reproductive physiology, foraging behavior, physical stress, and sampling error also likely influenced estimates.

Estimates of total DE intake and carrying capacity were likely highest during trial 1 and trial 7 because of increased biomass and precipitation. McCall (1988) related the highest carrying-capacity estimate in his study to amount of forage. He found that the enclosure with the highest percentage of available forage at the beginning of the trial also had the highest estimate. Drake and Palmer (1986) found the highest carrying capacity estimates in enclosures with the highest amount of available woody browse. Study deer were also in their third trimester of gestation during trials 1 and 7 and gained mass due to pregnancy.

Decreases in carrying capacity estimates during trial 2 were likely a result of decreases in both estimated biomass and precipitation, although additional factors may have affected estimates. Physiological stress caused from 4 of 12 females giving birth during trial 2 may have lowered estimates. Females were reweighed immediately after giving birth to fawns. However, the females continued to decrease in mass, which was likely related to parturition (e.g., uterine involution, etc.). Because all fawns were removed 2–5 days after birth, physiological stress from lactation likely did not influence results of later trials.

Carrying capacity estimates for trials 1, 2, and 7 may be biased because mass changes related to pregnancy may have masked mass changes due to changes in protein and fat reserves. During trials 1 and 7, deer may have lost mass from protein and fat reserves at the same time they gained mass from increasing fetal tissue and assorted fluids, which have little energy value. During trial 2, deer may have gained mass from increased protein and fat reserves as they lost mass from uterine involution. Pregnant deer should be avoided in future studies involving the tame deer technique. However, carrying capacity estimates then would not reflect what is happening with wild pregnant deer.

An additional cause for lower estimates may have resulted from a voluntary decrease in forage intake. Research in Louisiana (Fowler et al. 1967) and Texas

(Wheaton and Brown 1983) showed a decline in forage intake during summer. They related decreased intake to higher summer temperatures and humidity.

Foraging variability among individual deer and for the same deer among trials may have influenced estimates. Potts and Cowan (1983) found that tamer deer foraged more actively and lost the least mass. Tamer deer used in this study consistently lost less mass than other, wilder deer. Robinson (1962) found that white-tailed fawns occupying dominant positions in the hierarchy were better able to maintain physical condition. McCall (1988) suggested that the dominance hierarchy may have changed between trials in his study, causing differences in mass loss for individual deer. Additionally, Drake and Palmer (1986) reported that deer behavior influenced results in their study. We randomly selected deer for treatments after pairing by body mass and did not partition deer according to dominance hierarchy or tameness because of difficulties quantifying these traits.

Physical stress caused from capturing, transporting, and weighing deer may have varied between trials, causing variable estimates. Mautz and Fair (1980) found that induced physical stress more than tripled energy expenditure (kcal) in New Hampshire white-tailed deer. However, only physical stress caused by transporting deer was measured in our study. Mass change during transport varied from −1.0 to +0.3 kg ($\bar{x} = -0.3$ kg, SE = 0.4, $N = 15$).

The unique weighing process used in this study shortened weighing time and likely resulted in less psychic and physical stress. However, because of the treatment design and because several females were not sufficiently tame, it was not always possible to re-weigh all deer at each enclosure site during each trial. Deer within the supplementally-fed enclosures were especially difficult to re-weigh (in 6 of 42 cases, no final mass was measured), likely because of their exposure to supplemental feed and their reluctance to enter the weighing crate for access to shelled corn used as bait. When final mass could not be measured (7 of 84 cases), mass change could not be calculated. In such cases, only data from deer with a measured final mass were used in carrying capacity calculations. Failure to measure final mass in all cases may have biased our carrying capacity estimates upward. Deer that could not be re-weighed tended to be less tame. These deer may have lost more mass during trials because of this behavioral trait.

A final possible source of variation in carrying capacity estimates may be related to the minimum maintenance requirement value (159 kcal/kg$^{0.75}$/day) used in our calculations. This value was determined during winter in Pennsylvania (Clark, unpubl. data, Pa. State Univ.). The value compares favorably with calculations in Pennsylvania of 161 kcal/kg$^{0.75}$/day by Cowan and Clark (1981) and with calculations in Michigan of 160 and 158 kcal/kg$^{0.75}$/day by Ullrey et al. (1969, 1970). However, thermoregulatory costs of deer in southern Texas may not be as high as those of northern deer in winter. If maintenance requirements were actually lower during different seasons in Texas, our estimates may be biased downward. In addition, the DE equation would change, further complicating matters.

Our carrying capacity estimates were similar to converted estimates obtained by McCall (1988), which varied from 0.42 to 1.19 deer/ha ($\bar{x} = 0.85$). However, McCall's (1988) study was conducted in a different county, during winter and summer only, and study deer were not provided supplemental feed. Our estimates bracketed the long-term, adjusted (DeYoung et al. 1989) density estimates of 1.02 deer/ha obtained by helicopter on the refuge (Blankenship et al. 1994), further validating the tame-deer technique.

Our results suggested that carrying capacity changed dramatically from trial to trial. Past studies using the tame-deer technique also resulted in highly variable estimates (Potts and Cowan 1983, Drake and Palmer 1986). This variability is consistent with the concept that carrying capacity is a dynamic measure that fluctuates continually with changing environmental conditions. This variability also exposes the inadequacy of measuring carrying capacity on an annual basis. At a minimum, carrying capacity should be measured seasonally to more accurately determine lowest (limiting) and average carrying capacity levels. Limiting levels should be considered the standard measure of carrying capacity because it provides more useful information to the wildlife manager. Because of significant correlations between carrying capacity (deer/ha/year) estimates for supplemented enclosures and precipitation (cm), it appears that differences in precipitation alter carrying capacity in southern Texas.

Significant correlations of carrying capacity estimates with precipitation suggested that deer populations in southern Texas are not regulated solely by density-dependent factors. Gore et al. (1985) suggested that southern Texas deer populations tracked extremes in precipitation, declining during droughts and increasing when precipitation was adequate. Ruthven et al. (1994), found that female energy status, ovarian development, timing of breeding, fawn recruitment, and age structure were related to precipitation-caused changes in habitat quality in southern Texas. Blankenship et al. (1994) reported an increase in number of embryos found in females harvested during years of above-average rainfall. Similar dynamics are typical of large mammals in semi-arid environments (Gray and Simpson 1983, Caughley et al. 1987).

Correlation analysis indicated that precipitation, live biomass, dead biomass (negative correlation), forbs, and grass were parameters that should be included in a model predicting carrying capacity. Future research should test additional parameters not directly measured in this study (such as temperature and performed water in forage). The tame-deer technique appears promising in its ability to quantitatively measure carrying capacity on a year-round basis. However, the equation needs further refinement because of negative estimates obtained for individual deer.

Wildlife managers knowledgeable of the timing of environmentally stressful periods could artificially improve conditions to increase carrying capacity. Zaiglin and DeYoung (1989) found that free-ranging white-tailed deer in southern Texas consumed a higher rate of supplemental pellets during late summer than at other times of the year. They suggested that this increase contributed to increased fawn survival. Harvest strategies also could be adjusted according to estimates of carrying capacity measured during critical periods. With refinements in the tame-deer technique, wildlife managers may be able to estimate carrying capacity by estimating only biomass along permanent-transect lines or measuring precipitation. Biomass could be measured at seasonal or monthly intervals for more accurate management decisions.

Literature Cited

Bartmann, R. M. 1982. Evaluation of winter food choices by tame mule deer. J. Wildl. Manage. 46:807–812.

Blankenship, T. L., D. L. Drawe, and J. G. Teer. 1994. Reproductive ecology of white-tailed deer on the Welder Wildlife Foundation, Texas. Proc. Annu. Conf. Southeast. Assoc. Fish and Wildl. Agencies 48:69–77.

Box, T. W. and A. D. Chamrad. 1966. Plant communities of the Welder Wildlife Refuge. Contrib. 5, Ser. B. Welder Wildl. Found., Sinton, Texas. 28pp.

Caughley, G. 1976. Wildlife management and the dynamics of ungulate populations. Pages 183–246 *in* T. H. Croaker, ed. Applied biology. Vol. I. Acad. Press, London, U.K.

———, N. Shepherd, and J. Short. 1987. Kangaroos: their ecology and management in the sheep rangelands of Australia. Cambridge Univ. Press, New York, N.Y. 253pp.

Clark, A. C. 1977. Nutrient intake of white-tailed deer in winter and determination of the feeding capacity of deer range. Ph.D. Diss., Pa. State Univ., University Park. 95pp.

Cowan, R. L. and A. C. Clark. 1981. Nutritional requirements. Pages 72–86 *in* W. R. Davidson, F. A. Hayes, V. F. Nettles, and F. E. Kellogg, eds. Diseases and parasites of white-tailed deer. Tall Timbers Res. Sta. Misc. Publ. 7., Tallahassee, Fla.

DeYoung, C. A., F. S. Guthery, S. L. Beasom, S. P. Coughlin, and J. R. Heffelfinger. 1989. Improving estimates of white-tailed deer abundance from helicopter surveys. Wildl. Soc. Bull. 17:275–279.

Drake, W. E. and W. L. Palmer. 1986. Dormant season deer feeding capacity of northern hardwood forests. Pa. Game Comm., Fed. Aid in Wildl. Restor., Job Descrip. Rep. Proj. 04050. 41pp.

Drawe, D. L., A. D. Chamrad and T. W. Box. 1978. Plant communities of the Welder Wildlife Refuge. Second ed. Contrib. 5, Series B/Rev. Welder Wildl. Found., Sinton, Texas 38 pp.

Eberhardt, L. L. 1988. Testing hypotheses about populations. J. Wildl. Manage. 52:50–56.

Fowler, J. F., J. D. Newsom, and H. L. Short. 1967. Seasonal variation in food consumption and weight gain in male and female white-tailed deer. Proc. Southeast. Assoc. Game and Fish Comm. 21:24–32.

Gore, H. G., W. F. Harwell, M. D. Hobson, and W. J. Williams. 1985. Buck permits as a management tool in south Texas. Pages 149–163 *in* S. L. Beasom and S. F. Roberson, eds. Game harvest management. Caesar Kleberg Wildl. Res. Inst., Texas A&I Univ., Kingsville.

Gould, F. W. 1969. Texas plants, a checklist and ecological summary. Tex. Agric. Exp. Sta. Tech. Bull No. 585. 121 pp.

Gray, G. G. and C. D. Simpson. 1983. Population characteristics of free-ranging Barbary Sheep in Texas. J. Wildl. Manage. 47:954–962.

Guckian, W. J. and R. N. Garcia. 1979. Soil survey of San Patricio and Aransas counties, Texas. U.S. Dep. Agric., Soil Conserv. Serv., Washington, D.C. 122pp.

Gysel, L. W. and L. J. Lyon. 1980. Habitat analysis and evaluation. Pages 305–327 *in* S. D. Schemnitz, ed. Wildlife techniques manual. The Wildl. Soc, Washington, D.C.

Hobbs, N. T. and D. M. Swift. 1985. Estimates of habitat carrying capacity incorporating explicit nutritional constraints. J. Wildl. Manage. 49:814–822.

Mautz, W. W. 1978. Nutrition and carrying capacity. Pages 321–328 *in* J. L. Schmidt and D. L. Gilbert, eds. Big game of North America. Stackpole Books, Harrisburg, Pa.

——— and J. Fair. 1980. Energy expenditure and heart rate for activities of white-tailed deer. J. Wildl. Manage. 44:333–342.

McCall, T. C. 1988. Comparison of tame-deer enclosures and forage analysis for determining the carrying capacity of white-tailed deer. M.S. Thesis, Texas A&I Univ., Kingsville 124pp.

———, R. D. Brown, and L. C. Bender. 1997. Comparison of techniques for determining the nutritional carrying capacity for white-tailed deer. J. Range Manage, 50:33–38.

McCullough, D. R. 1979 The George Reserve deer herd. Univ. Michigan Press, Ann Arbor. 271pp.

———, D. S. Pine, D. L. Whitmore, T. M. Mansfield, and R. H. Decker. 1990. Linked sex harvest strategy for big game management with a test case on black-tailed deer. Wildl. Monogr. 112:1–41.

Meyer, M. W., R. D. Brown, and M. W. Graham. 1984. Protein and energy content of white-tailed deer diets in the Texas Coastal Bend. J. Wildl. Manage. 48:527–534.

Norwine, J. and R. Bingham. 1985. Frequency and severity of droughts in south Texas: 1900–1983. Pages 1–17 *in* R. D. Brown, ed. Livestock and wildlife management during drought. Caesar Kleberg Wildl. Res. Inst., Texas A&I Univ., Kingsville.

Olson-Rutz, K. M. and P. J. Urness. 1987. Comparability of foraging behavior and diet selection of tractable and wild mule deer. Publ. 88-3, Utah Div. Wildl. Resour., Salt Lake City. 39pp.

Potts, R. R. and R. L. Cowan. 1983. Evaluation of dormant season feeding capacity of deer habitats from digestible intake estimates. Dep. Dairy and Anim. Sci., Pa. State Univ., University Park, unpubl. rep. 21pp.

Robinson, W. L. 1962. Social dominance and physical condition among penned white-tailed deer fawns. J. Mammal. 43–462–469.

Ruthven, D. C., E. C. Hellgren, and S. L. Beasom. 1994. Effects of root plowing on white-tailed deer condition, population status, and diet. J. Wildl. Manage. 58:59–70.

SAS Institute, Inc. 1985. SAS User's guide: statistics. SAS Inst., Inc., Cary, N. C. 956pp.

Shea, S. M., T. A. Breault, and M. L. Richardson. 1992. Herd density and physical condition of white-tailed deer in Florida flatwoods. J. Wildl. Manage. 56:262–267.

Ullrey, D. E., W. G. Youatt, H. E. Johnson, L. D. Fay, B. L. Schoepke, and W. T. Magee. 1969. Digestible energy requirements for winter maintenance of Michigan white-tailed does. J. Wildl. Manage. 33:482–490.

———, ———, ———, ———, ———, and ———. 1970. Digestible and metabolizable energy requirements for winter maintenance of Michigan white-tailed does. J. Wildl. Manage. 34:863–869.

Varner, L. W., L. H. Blankenship, and G. W. Lynch. 1977. Seasonal changes in nutritive value of deer food plants in south Texas. Proc. Annu. Conf. Southeast. Assoc. Fish and Wildl. Agencies 31:99–106.

Wheaton, C. and R. D. Brown. 1983. Feed intake and digestive efficiency of south Texas white-tailed deer. J. Wildl. Manage. 47:442–450

Zaiglin, R. E. and C. A. DeYoung. 1989. Supplemental feeding of free-ranging deer in south Texas. Texas J. Agric. and Nat. Resour. 3:39–41.