ESTIMATION OF BODY WEIGHT OF WHITE-TAILED DEER (ODOCOILEUS VIRGINIANUS) FROM BONE SIZE

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ABSTRACT.—Lower leg bones of 210 modern white-tailed deer (Odocoileus virginianus) from 8 localities in eastern North America were used to examine factors influencing the relationship between bone size and body size. Locality (island versus mainland), age, and sex were shown to affect bone size-body weight relationships. After accounting for the compounding factors, a set of unified regressions are presented that estimate adult live weight in the late autumn of white-tailed deer. However, since live weight is subjected to many diverse influences, the estimates should be used only as an ordinal guide to size.

INTRODUCTION

White (1953) pioneered the use of the minimum number of individuals (MNI) and meat weight to characterize the animal portion of human subsistence. In White's system, the MNI of each prey species was multiplied by its "average" meat weight (a percentage of average body weight), producing an index that indicated the relative contribution of each species to human diet. Although both MNI and meat weight became widely used in archaeozoological analyses, their shortcomings also became apparent. Problems associated with, and suggested alterations to, MNI have been addressed in a number of studies (Casteel 1977; Grayson 1973, 1978, 1979; Martin 1983; for reviews, see Grayson 1984; Klein and Cruz-Uribe 1984). Fieller and Turner (1982) proposed a probabilistic alternative to MNI (but see, Klein and Cruz-Uribe 1984).

Few studies have critically evaluated "average" meat weights. However, Smith (1975) noted the effects that sex, age, and location have on weight in white-tailed deer (Odocoileus virginianus). After (1) showing that deer from a study site had a balanced sex ratio and (2) determining the age profile from tooth eruption and wear of the mandibles, Smith (1975) used sex-pooled, age-specific mean dressed weights of the modern local deer to produce meat weight estimates. Emerson (1978, 1983), taking another approach, estimated dressed weights of deer from archaeological contexts using a regression that related the length of the astragalus to dressed weight in a sex- and age-pooled sample of modern white-tailed deer.

Recent reviews of the quantification techniques commonly used in archaeozoological analyses have noted the numerous biases and deficiences of methods, in general, and of meat weight, in particular (Grayson 1984; Klein and Cruz-Uribe 1984; Lyman 1979). Lyman (1979) notes confusion in the terminology of various weight measures (e.g., live weight, available meat, consumed meat) and advocates the use of butchering units. Klein and Cruz-Uribe (1984) dismiss meat weight as adding no significant new information about the relative importance of various taxa at a site, while Grayson (1984) takes the view that meat weight based on MNI (as opposed to bone weight) may have some validity as an ordinal measure of faunal usage. PURDUE

Even though the use of estimated meat weight as traditionally applied may have limited utility, certain other research problems can still benefit by reliable projections of live or body weight (leaving to others the decision of what proportion of weight to allocate to available and to consumed meat). For example, biomass, or its conversion to calories, can be used to evaluate the benefits of many theoretical cost-benefit models of human subsistence (Earle and Christenson 1980). Since some animal species are known to show shifts in body size through time in the Holocene (Purdue 1980, 1986), then those shifts may require consideration in such models. Measures (e.g., bone width, factor scores based on morphological measurements) other than live weight, or calories derived from body weight, cannot easily be compared between taxa. Future studies that contrast the relative contributions of plant and animal resources to human diet (currently an important, but neglected issue) may find derived calories from meat weight an important measure, in spite of its many faults.

The objectives of this study are to thoroughly examine the relationship between bone measurement and live weight in white-tailed deer, an important terrestrial prey item of prehistoric humans in eastern North America, and, after accounting for as many sources of variation as possible, to present equations that accurately estimate live weight.

METHODS

The lower legs of 207 deer from 8 localities were collected when the animals were brought to hunter check stations. Three additional specimens were killed by automobiles in central Illinois (Table 1). All animals were taken in the late fall or early winter. Live or dressed weight (to the nearest 0.45 kg), sex, and age (determined by tooth eruption

No. of Adults ^a					
Locality	Male	Female	Dates Sampled		
Savannah River Plant, South Carolina	3	35b	late Nov/early Dec 1980		
Ossabaw Island, Georgia	_	22	18-20 Dec 1980		
Hickory County, Missouri	2	7	18-19 Nov 1977		
Macon County, Missouri	2	6	18-19 Nov 1977		
Ozark County, Missouri	1	11	18-19 Nov 1977		
Pope County, Illinois	1	13	18-19 Nov 1977		
Illinois (central area)	0	3	Nov 1976; Feb 1977		
Arkansas (statewide)	5	25	7-9; 27-28 Nov 1981		

TABLE 1.—List of localities sampled for modern white-tailed deer.

^amales \geq 3.5 yr.; females \geq 2.5 yr.

^ban additional 74 non-adults were used for some tests

and wear) were noted for each specimen. Dressed weights, which were taken for the majority of specimens from the Missouri localities, Pope County, Illinois, and Arkansas, were converted to live weights using sex- and age-specific regressions (Roseberry and Klimstra 1975). Live weights were directly taken on specimens from South Carolina and Georgia. An additional sample of 24 deer was taken from hunters in Jo Daviess County, Illinois. No weights were available for these animals, but they were useful for testing the consistency of the weight-estimating regressions between measurement sets.

Nine measurement sets on 7 bones were made to the nearest 0.01 mm using handheld calipers (Fig. 1). The measurements were on ends of long bones or small, compact foot bones that are commonly recovered from archaeological sites. Gingerich *et al.* (1982)

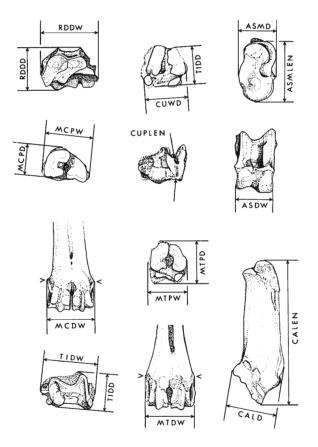


FIG. 1.—Measurements taken on leg bones of white-tailed deer. Abbreviations are: ASDW, distal width of the astragalus; ASMD, medial depth of the astragalus; ASMLEN, medial length of the astragalus; CALD, lateral depth of the calcaneum; CALEN, length of the calcaneum; CUDD, distal depth of the cuboid; CUPLEN, plantar length of the cuboid; CUWD, distal width of the cuboid; MCDW, distal width of the metacarpal; MCPD, proximal depth of the metacarpal; MCPD, distal width of the metacarpal; MTDW, distal width of the metatarsal; MTPD, proximal depth of the metatarsal; MTPD, proximal depth of the metatarsal; MTPD, distal depth of the radius; RDDW, distal width of the metatarsal; RDDD, distal depth of the radius; RDDW, distal width of the radius; TIDD, distal depth of the tibia; and TIDW, distal width of the tibia.

PURDUE

found that the crown tooth area (tooth length x width) of primates improved the estimation of body weight, relative to that calculated from simple linear measurements. Preliminary analyses of the post-cranial bones of deer yielded similar results and, consequently, cross-sectional areas or element volumes were used where possible (Table 2). For the distal ends of the metacarpal and metatarsal, preliminary analysis indicated that the depth measurements were affected by continual resculpturing of the bone long after the closing of the epiphyseal suture. Thus, it was not possible to use cross-sectional area as a measure for these elements.

Several statistical procedures were used to demonstrate the effects of biological age, sex, and locality on the relationship between bone size and body weight. Except for the age analysis, which is graphically depicted, all bone size and body weight data were

TABLE 2.—Formulae for converting measurements into areas and volumes. Measurement abbreviations are given in Fig. 1. Abbreviations for measurement sets are: RDAR, cross-sectional area of the distal end of the radius; TIAR, cross-sectional area of the distal end of the tibia; MCPAR, cross-sectional area of the proximal end of the metacarpal; MTPAR, cross-sectional area of the proximal end of the metatarsal; ASVO, volume of the astragalus; CUVO, volume of the cuboid; and CAAR, area of the lateral surface of the calcaneum.

Element (end)	Approximate Shape	Formula
Radius (distal)	ellipse	$RDAR = \frac{RDDW}{2} \times \frac{RDDD}{2} \times \pi$
Tibia (distal)	ellipse	$TIAR = \frac{TIDW}{2} \times \frac{TIDD}{2} \times \pi$
Metacarpal (proximal)	ellipse	MCPAR = $\frac{MCPW}{2} \times \frac{MCPD}{2} \times \pi$
Metacarpal (distal)	line	MCDW
Metacarpal (distal)	ellipse	$MTPAR = \frac{MTPW}{2} \times \frac{MTPD}{2} \times \pi$
Metatarsal (distal)	line	MTDW
Astragalus	Elliptical cylinder	ASVO = $\frac{\text{ASMD}}{2} \times \frac{\text{ASMLEN}}{2} \times \text{ASDW} \times \pi$
Cuboid	elliptical cylinder	$CUVO = \frac{CUWD}{2} \times \frac{CUDD}{2} \times CUPLEN \times \pi$
Calcaneum	ellipse	$CAAR = \frac{CALEN}{2} \times \frac{CALD}{2} \times \pi$

transformed with natural logarithms (Gingerich *et al.* 1982; Reitz and Cordier 1983). Regression analyses, conducted with the GLM Procedure of SAS (Helwig and Council 1979), were used to test the effects of sex and location on estimating weight. The REGRES-SION option in SPSS (Nie *et al.* 1975) was used to produce the final regressions for predicting body weight.

RESULTS

Effect of ontogeny.—Deer of all ages from the Savannah River Plant, South Carolina were used to indicate that bones and body weight differ in growth rate (Fig. 2). The bones of the lower leg reach adult proportions much earlier in an animal's life than does body weight. In females, approximately 90% of adult bone size is reached at 6 mo. of age, whereas only 60% of the final body weight is amassed. Similar growth patterns are apparent in males, although the entire growth process is extended at least one year longer than in females. Unfortunately, the exact nature of the curves for males is not known because few males ≥ 42 mo. were available for study. Since the growth rates for bones and body weight are fundamentally different, all subsequent analyses used only animals that had achieved maximum growth, ie., females ≥ 30 mo. and males ≥ 42 mo. Males 42 mo. old have not reached their maximum weight (Severinghaus 1979), but, because of the small sample size, they were used in portions of the remaining study.

Effect of locality.—Females from Ossabaw Island, Georgia; Savannah River Plant, South Carolina; Macon and Hickory counties, Missouri; and Pope County, Illinois, were used to test if locality influenced the relationship between bone size and body weight (Table 3). Slopes are unaffected by locality. However, the Y-intercept is heterogeneous in tests of all 9 measurement sets when 5 localities are included. Significance levels for the pairwise tests of differences due to locality indicate that the Ossabaw Island sample consistently differs from two or more of the mainland samples. Brisbin and Lenarz (1984) reported other proportional differences between deer from Ossabaw Island and mainland South Carolina. They were unable to resolve which of the differential traits were phenotypic responses to environment and which were the result of natural selection.

The analyses were repeated with Ossabaw Island deer excluded (Table 3). As before, all slopes are homogeneous, but this time 6 of 9 Y-intercepts are homogeneous. Significant differences in Y-intercepts occur for the distal end of the tibia, proximal end of the metatarsal, and the cuboid. The pairwise tests indicate that the differences are between Macon County, Missouri, and the Savannah River Plant, South Carolina.

The mainland samples of deer were reasonably, but not absolutely, homogenous in the relationships between bone size and body weight. The island deer are excluded from further analyses.

Effect due to sex.—Analyses of covariance were applied to test the influence of sex on bone size-body weight relationships (Table 4). Slopes are homogeneous between the sexes on all tests. In contrast, the Y-intercepts, except for that associated with the distal end of the metacarpal, are significantly different.

Bone size-body weight regressions.—The results described above indicate it prudent to estimate body weight from sex-specific regressions based on adult deer from the mainland (Table 5). It is, however, rarely possible to control all these factors with deer remains from archaeological sites. Thus, Table 5 also contains regressions with the sexes combined (females 30 mo. old were deleted to achieve a better balanced sample size between the sexes).

The use of the regressions in Table 5 for estimating body weight is demonstrated with adult female deer from Jo Daviess County, Illinois, and the Savannah River Plant,

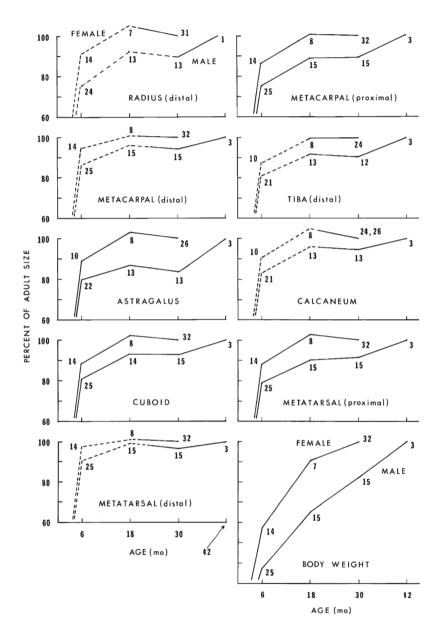


FIG. 2.—Growth of the leg bones and body weight of white-tailed deer from the Savannah River Plant, South Carolina. Females are represented by the upper curve on each graph. The dashed portion of a curve indicates unfused epiphyseal plates (Purdue 1983a). Percentages are based on cross-sectional area for the radius (distal end), metacarpal (proximal end), tibia (distal end), calcaneum, and metatarsal (proximal end); on volume for the astragalus and cuboid; on one linear measurement for the metacarpal (distal end) and metatarsal (distal end); and on kg for body weight. Sample sizes are indicated by each point (dual sample sizes mean one or more specimens could not be measured for one variable).

TABLE 3.—Regression analyses testing the effect of locality on the bone size-body weight relationship. Adult females from 5 localities (Series 1: Ossabaw Island, Georgia [OS]; Savannah River Plant, South Carolina [SC]; Pope County, Illinois [PO]; and Macon [MA] and Hickory [HI] counties, Missouri) or from 4 localities (Series 2: exclude Ossabaw Island) were used. On each series of localities, two analyses per measurement set were performed: the first tested for the homogeneity of slopes. Only probabilities are reported. If not significant at the 0.05 level, a second analysis examined homogeneity of Y-intercepts (critical probability <0.05). Significant probabilities are indicated by a *. Also indicated are pairs of localities that showed significant differences in adjusted means. Abbreviations are given in Table 2.

Measurement		Prob	ability		
Set	Series	Slope	Y-intercept	Significant Pairs	
RDAR	1	0.73	0.00*	OS-PO; OS-SC	
	2	0.47	0.60		
TIAR	1	0.31	0.00*	OS-PO; OS-MA; OS-HI; OS-SC; HI-SC	
	2	0.66	0.02*	MA-SC	
MCPAR	1	0.25	0.00*	OS-PO; OS-MA; OS-SC	
	2	0.50	0.06		
MCDW	1	0.74	0.00*	OS-PO; OS-MA; OS-HI; OS-SC	
	2	0.59	0.14		
MTPAR	1	0.16	0.00*	OS-PO; OS-MA; OS-SC	
	2	0.37	0.03*	MA-SC	
MTDW	1	0.08	0.01*	OS-MA; OS-SC	
	2	0.27	0.08		
ASVO	1	0.09	0.00*	OS-PO; OS-MA; OS-HI; OS-SC	
	2	0.46	0.06		
CUVO	1	0.74	0.00*	OS-PO; OS-MA; OS-HI; OS-SC	
	2	0.75	0.04*	MA-SC	
CAAR	1	0.18	0.01*	OS-PO; OS-MA' OS-HI; OS-SC	
	2	0.18	0.09		

South Carolina (Table 6). Admittedly, the latter deer were part of the sample upon which the regressions were based, but, since independent specimens of known weight were lacking, the use of the Savannah deer must suffice. The sex-specific regressions applied to the South Carolina deer successfully estimated actual body weight. Also, the regressions consistently indicated that the Illinois deer were significantly larger than those from South Carolina. Finally, the combined-sex regressions for Jo Daviess County deer yielded slightly higher, significant weight estimates when compared to sex-specific values.

PURDUE

TABLE 4.—Regression analyses testing the effect of sex on the bone size-body weight relationship. Two analyses per measurement set were performed: the first tested for the homogeneity of slopes. Only probabilities are reported. If not significant at the 0.05 level, a second analysis examined homogeneity of Y-intercepts (critical probability <0.05). Significant probabilities are indicated by a *. Abbreviations are given in Table 2.

Measurement	Pro	bability
Set	Slope	Y-intercept
RDAR	0.45	0.02*
TIAR	0.56	0.00*
MCPAR	0.59	0.00*
MCDW	0.27	0.07
MTPAR	0.60	0.00*
MTDW	0.27	0.00*
ASVO	0.15	0.00*
CUVO	0.60	0.00*
CAAR	0.48	0.00*

DISCUSSION

The weight of a deer at any particular time is the net result of many factors, some of which can and some of which cannot be controlled in archaeological contexts. Transient changes in weight, such as seasonal shifts in fat deposits and year-to-year variation, cannot be addressed given the resolution presently derivable from archaeological data. For instance, the amount of stored fat can fluctuate faster (Moen and Severinghaus 1981) than most seasonal indicators are able to detect change (Morey 1983). Body weight can vary up to $\pm 30\%$ annually due to accumulation and depletion of fat stores, as dictated by forage conditions, weather severity, photoperiod, and other physiological fluctuations, e.g., pregnancy (Moen and Severinghaus 1981). Similarly, year-to-year variation in body weight of deer of like sex and age, sampled in late fall, can vary significantly (Kirkpatrick *et al.* 1976). Changes such as these leave no markers in bone remains, but even if they did, the temporal control of virtually all archaeological sites is insufficient to make sense of the resultant patterns. Although transparent to us through studies on bone, these transient factors could have been critical for prehistoric deer hunters.

In contrast to transient fluctuations in weight, bones of modern deer can reflect the effects of sex and ontogenetic age on body weight, but the picture is more complicated than indicated in previous studies (e.g., Emerson 1983). Differential growth of body parts, particularly the rapid development of lower leg bones relative to the slow accumulation of body weight, makes the estimation of weight for young deer inaccurate, as was also noted, but not fully explored, by Emerson (1978). Estimates based on elements with fused epiphyseal plates are more trustworthy, but even here, body weight often continues to increase after the time of fusion. Realistic estimates of weight are further complicated by the sexes differing in their relationships between bone size and body weight. Unfortunately, post-cranial deer bones from archaeological sites can only rarely be assigned sex and ontogenetic age (but, for an exception, see Purdue 1983b).

The reference sample of deer in the current study was diverse, covering portions of five states. Fortunately, once the Ossabaw Island specimens were deleted, no con-

Measure- ment Set	Sex	In A	В	N	sy	r2	F
RDAR	М	-2.97198	1.07685	11	0.07705	0.83	45.1***
	F	-1.92477	0.90382	95	0.10543	0.56	117.6***
	Both	-3.34697	1.12422	11,35	0.11132	0.74	122.9***
TIAR	М	-5.90302	1.52647	13	0.09687	0.76	32.2***
	F	-4.80119	1.34048	78	0.10485	0.60	112.7***
	Both	-7.23944	1.72084	13,31	0.10888	0.79	156.4***
MCPAR	Μ	-3.39005	1.22741	13	0.09672	0.75	32.4***
	F	-2.65716	1.08655	97	0.10794	0.53	108.1***
	Both	-4.68886	1.42989	13,36	0.12336	0.70	111.5***
MCDW	М	-5.11833	2.71314	13	0.08827	0.79	41.1***
	F	-3.23203	2.14051	97	0.10094	0.59	137.2***
	Both	-4.46664	2.51464	13,36	0.11734	0.73	128.2***
MTPAR	м	-5.27456	1.48019	13	0.08622	0.82	48.7***
	F	-4.46255	1.32736	87	0.11124	.058	116.5***
	Both	-6.69049	1.68850	13,33	0.12777	0.73	120.5***
MTDW	М	-5.52915	2.81534	13	0.09660	0.77	36.6***
	F	-3.52154	2.19842	97	0.11069	0.56	123.1***
	Both	-5.11749	2.68206	13,36	0.13243	0.70	109.6***
AVSO	М	-8.13984	1.26867	13	0.06957	0.88	80.8***
	F	-4.62775	0.88870	80	0.12435	0.50	76.6***
	Both	-9.49655	1.40109	13,31	0.11862	0.78	148.6***
CUVO	М	-3.54197	0.87090	13	0.13959	0.49	10.6**
	F	-2.55390	0.73732	86	0.12306	0.45	70.1***
	Both	-5.05259	1.03017	13,33	0.14936	0.59	63.2***
CAAR	Μ	-3.33992	0.98336	11	0.15156	0.31	4.1ns
	F	-5.75054	1.27511	76	0.11429	0.54	85.9***
	Both	-8.40131	1.63313	11,30	0.14471	0.63	65.8***

TABLE 5.—Regressions for estimating body weight from bone size of white-tailed deer. Separate equations are presented for females (\geq 30 mo.), for males (\geq 42 mo.), and for combined sexes (males and females \geq 42 mo.). See Table 2 for measurement set abbreviations; probability abbreviations are: ns, non significant; **, P 0.01; and ***, P 0.001.

sistent difference in the bone size-body weight relationship was noted, thus moderating Emerson's (1983) concern that modern deer outside of south-central Wisconsin, the origin of his sample, might show a different bone-weight relationship. However, clinal variation through time, which is now known to affect deer (Purdue 1986), impacts the utility of Smith's (1975) method for estimating body weight. Smith suggested equating weights of like sex and age classes of archaeological and modern deer from the same locality. Given the dynamic nature of deer size (Purdue 1986), the ability to choose a suitable modern analog is diminished.

TABLE 6.—Comparison of actual adult female weight and that estimated from bone size. The samples originated from Jo Daviess County, Illinois (N = 24), and the Savannah River Plant, South Carolina (N = 24). The weight was estimated for each individual deer, then descriptive statistics were calculated (the mean in kg and the standard deviation in parentheses are shown). Separate estimates were made using each bone element and regression model (Table 5). See Table 2 for abbreviations.

Measurement	South Carolina	Jo Daviess Co., Illinois		
Set	Sex-specific	Sex-specific	Combined-sex	
RDAR	43.06 (2.75)	59.36 (3.38)	62.01 (4.40)	
TIAR	45.30 (3.99)	60.41 (5.04)	66.41 (7.00)	
MCPAR	43.78 (4.03)	57.38 (4.20)	62.69 (6.00)	
MCDW	44.14 (3.45)	59.28 (4.77)	61.79 (5.80)	
MTPAR	45.29 (4.64)	58.07 (4.48)	63.68 (6.23)	
MTDW	45.05 (3.78)	60.10 (5.23)	65.17 (6.89)	
ASVO	44.44 (4.15)	57.07 (6.06)	65.39 (11.16)	
CUVO	45.29 (4.09)	56.92 (4.71)	65.24 (8.26)	
CAAR	45.51 (3.66)	58.34 (4.42)	64.90 (6.33)	
Actual Body				
Weight	44.60 (6.38)			

Summary of analyses of variance:

- 1. A one-way anova showed no significant differences in the series from South Carolina that included estimates from different measurement sets and actual body weight.
- 2. A two-way anova indicated significant differences between sex-specific estimates between South Carolina and Jo Daviess Co., Illinois, but no significant differences among measurement sets or the interaction term.
- 3. A two-way anova indicated significant differences between sex-specific and combinedsex estimates for Jo Daviess Co., Illinois, but no differences among measurement sets or the interaction term.

In spite of numerous limitations, estimates of the body weight of prey species contributes an added perspective to the interpretation of human subsistence. For example, measurements of astragali of deer from central Illinois indicated size shifts through time have occurred (Purdue 1986). When these measurements are converted to body weight, a sense of the magnitude of the difference between time periods can be achieved. Late Archaic inhabitants of the Pabst Site (DeWitt County) took adult bucks and does that averaged 77.7 and 52.2 kg., respectively. Nearby, but 3,000 years later, residents of the Crable Site (Fulton County) hunted bucks that weighed 102.0 kg. and does that weighed 60.4 kg. The resultant difference in yield (24% for males and 14% for females) suggests that the size factor within a prey species could be a consideration in human procurement strategies.

It is imprudent to consider any archaeological bone-based estimate of body weight reflective of reality. Rather, an estimate should be viewed as an index that smooths multiple compounding factors and is useful only in an ordinal sense, not unlike that suggested by Grayson (1984) in a slightly different context. The present study attempted to isolate and to evaluate the relative impact of the various compounding factors so that the limits of body weight estimates would be better known. In that context, use of either Emerson's (1978, 1983) regression based on astragalus length or the set of equations presented in this study is satisfactory, although the latter system has certain advantages:

- 1. Estimates of weight are based on more than one measurement on an element, which, in most cases, compensate for vagaries that can affect a single measurement.
- 2. Better control and greater sample size were maintained for the reference deer.
- 3. Log-log transformations of original data improved the fit of linear regressions (e.g., Gingerich *et al.* 1982).
- 4. Weight estimates are possible based on any one of nine measurement sets representing seven elements in a unified system that yields consistent results. Thus, weights of deer from different sites, or from within the same site, can be compared, even though the estimates may be based on different bones.
- 5. Possible effects of geographic variation were taken into account.

Other methods, namely White's (1953) and Smith's (1975), although important contributions in their time, probably should be no longer used.

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