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Author(s): Allen E. Anderson and E. Medin
Source: *The Journal of Wildlife Management*, Vol. 33, No. 3 (Jul., 1969), pp. 520-533
Published by: Wiley on behalf of the Wildlife Society
Stable URL: https://www.jstor.org/stable/3799374
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Received for publication September 13, 1968.

ANTLER MORPHOMETRY IN A COLORADO MULE DEER POPULATION[1]

ALLEN E. ANDERSON, Research Center, Colorado Division of Game, Fish, and Parks, Fort Collins
DEAN E. MEDIN,[2] Research Center, Colorado Division of Game, Fish, and Parks, Fort Collins

Abstract: Symmetry was demonstrated between left and right antler beam diameters, lengths, and number of points in over 1,200 Cache la Poudre mule deer (*Odocoileus hemionus*) segregated into two age-classes. Decreasing annual precipitation, soil moisture, and three- to five-fold decreases in mean yields of two major winter range browse species over a 4-year period did not appear to affect antler development. Simple correlation coefficients (r) of antler beam weight (Y) versus antler beam measurements (X) of 25 yearling deer were: diameter, 0.62; length, 0.82; and number of points, 0.49. Similar values for 30 deer about 27 months and older were: diameter, 0.82; length, 0.74; and number of points, 0.52. Multiple correlation coefficients derived from antler weight versus these variables were: 0.87 (yearlings) and 0.82 (adults). Antler weight was linearly related to estimated age (0.94), and nonlinearly to eviscerated carcass weight (0.85) in 23 mule deer ranging in age from about 15–77 months. The limitations and possible management applications of these data are described.

There are no published statistical descriptions of antler morphometry in Rocky Mountain mule deer based on large, age-related samples from a single population. Cowan (1936:208–209) described the antlers and gave detailed measurements of the left beam from five Rocky Mountain mule deer of unstated age from the Pacific Coast. Hunter (n.d.:9) listed the means and extremes of several measurements from both beams and empirically related these to age-class, carcass weight, and several carcass measurements sampled from four Rocky Mountain mule deer populations in Colorado. His sample sizes ranged from 1–158 when segregated into five age-classes. Russo (1964: 110) gave the minimum number of points on one antler and the frequency of three antler-spread classes for over 3,000 Kaibab North, Arizona mule deer.

The apparent assumption of most authors that the left and right antler beams do not differ significantly in measurable attributes has not been tested. That this assumption may be invalid was suggested by the work of Riney (1954:575–576). He found that in a local New Zealand population of fallow deer (*Dama dama*), there was a definite tendency for the right beam to be larger than the left, both in successive sets from two captive deer and in 29 sets from a free-ranging population.

It has been postulated that antler shape is due largely to genetic factors whereas relative antler size of a given age-class is related directly to nutritional levels (Taber and Dasmann 1958:17). The apparent relationship between seasonal nutritional levels

[1] A contribution from Colorado Federal Aid Project W-105-R.
[2] Present address: Intermountain Forest and Range Experiment Station, Boise, Idaho.

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and antler development in white-tailed deer (*O. virginianus*) has been demonstrated experimentally by French et al. (1956), and in general terms of population density-forage abundance interactions of free-ranging populations by Park and Day (1942), Severinghaus et al. (1950), Dahlberg and Guettinger (1956), and Banasiak (1961). Huxley (1931:853) reviewed some of the early European work which seemed to indicate that poor antler development in roe deer (*Capreolus capreolus*) was related to severe winters and presumably a quantitative lack of forage as well as to apparent regional deficiencies in calcium levels. There are few similar published studies of migratory mule deer. Swank (1958:18) reported that about 52 percent of a check station sample of Kaibab North mule deer were "spikes," following two consecutive summers of critical range conditions, as compared to 12.5 percent the previous year with presumably good summer range condition. Taber (1958) suggested that the antler development of yearlings may reflect winter nutritional levels occurring during the previous winter and thus aid in assessments of winter range.

Probably the best measure of antler development is the total weight of one or both beams, but the use of mature deer antlers as trophies has prevented a large sampling. Therefore, the linear measurement(s) most closely related to antler weight, having the least inherent variability, will provide the best estimate of average antler development. These have not been described for mule deer. Linsdale and Tomich (1953:20) provided extensive statistical descriptions of the length, diameter, and weight of single beams from a black-tailed deer (*O. h. columbianus*) population but did not relate linear antler measurements to weight.

The allometry of antlers in North American cervids has received scant attention. If antler weight is closely related to age or carcass weight, regression equations of these relationships have management potential.

This paper describes and compares left and right antler beam measurements of Rocky Mountain mule deer by age-class, relates these measurements to precipitation and browse yields, and provides correlation analyses of beam weight-measurement relationships and total antler weight as a function of carcass weight and age.

We thank the many individuals who assisted in the field and laboratory: particularly F. Abelard, B. Baker, R. Buhler, G. Carlson, T. E. Hakonson, W. E. Jones, Jr., O. D. Markham, D. Minnich, L. Nelson, Jr., K. E. Nicolls, K. A. Porter, W. F. Wallace, and J. Wolloch. Most of the analyses were performed on an IBM 1401 digital computer by G. Beck and B. Duran under the supervision of D. C. Bowden of the Colorado State University Statistical Laboratory, Fort Collins.

STUDY AREA AND POPULATION

All data were obtained from 1960–1965, during the course of an ecological investigation of the mule deer inhabiting about 528 square miles of the Cache la Poudre River drainage within or adjacent to Roosevelt National Forest in north central Colorado. This South Platte tributary originates along the Continental Divide and flows easterly through the Front Range. The drainage pattern is dendritic through generally rugged to precipitous, plutonic terrain. Elevations range from about 5,500 ft to over 12,000 ft. Soils are primarily greywooded and rockland (Anonymous 1964) and derived mainly from schist–gneiss, schist, granitic, and igneous rock with some sedimentary formations at the lower elevational limits (Lovering and Goddard 1950).

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Costello (1954) has described the elevational sequence of Front Range vegetative zones and their plant communities. Dietz et al. (1962:12) listed the conspicuous plants within the Cache la Poudre drainage. Loveless (1967) has provided a detailed environmental analysis of upper Cache la Poudre winter range.

The Cache la Poudre mule deer population is migratory, but average summer population-density indices on the winter range (below about 8,500 ft elevation) ranged from about 5–25 deer per square mile compared to winter density indices of about 25–60 deer per square mile. Minimum winter range harvest densities ranged from less than one to about nine deer per square mile. About 65–70 percent of six annual harvest samples consistently occurred on about 18 percent of the total yearlong range. Evidence of excessive browse use was rare and localized during the period of study.

METHODS AND MATERIALS

Antler Measurements

Completely developed mule deer antlers were measured from two samples. The first resulted from a continuous voluntary check station sample taken 12–16 hr during each of 58 days over six regular hunting seasons. Season lengths ranged from 5–16 days and averaged about 10 days. The second sample was a twice monthly collection of mule deer shot throughout the drainage from 1961 to 1965. Their antlers were examined in the laboratory. At the check station, deer were placed in one of six age-classes on the basis of tooth replacement and wear (Robinette et al. 1957). Since a 1966 check station study indicated that substantial error occurred in aging mule deer of about 40 months and older (Erickson 1967), these data were combined into three broad age-classes: 16–18 months, 28–30 months, and 40 or more months, for analysis. Significance tests were limited to the 16–18-month- and 28–30-month-old deer. In the laboratory, deer ages were estimated to the nearest month by the dental-cementum technique as modified by Erickson (1967), and by assuming a June birth date for this population (Anderson and Medin 1968). Brow tine lengths and antler weights were not obtained for the check station sample, but the following measurements and observations were made on both samples as modified from the Boone and Crockett Club (1958).

Beam Diameter.—Measured on both beams with a vernier caliper to the nearest mm at a point 2.5 cm above the burr or corona. The calipers were held so that the longitudinal axis of the caliper was perpendicular to the longitudinal axis of the head. Bone protuberances were avoided if possible. This measurement was used both because previous experience had indicated that the beam circumference measurements stipulated by the Boone and Crockett Club (1958) were difficult to measure accurately under check station conditions and the beam diameter measurement had been widely used in Colorado (Hunter n.d.) and elsewhere (Severinghaus et al. 1950).

Beam Length.—Measured on both beams with a flexible steel tape to the nearest cm along the outer surface of the main beam from the burr to the tip of the lowest and most anterior portion.

Inside Spread.—Measured with a flexible steel tape to the nearest cm at the point of maximum distance between the main beams.

Number of Antler Points.—The antler appendages, 2.5 cm or more in length, were counted and recorded for each beam. The brow tines were excluded.

Brow Tine.—The presence or absence of this basal structure was noted and recorded

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for each beam. The length was measured to the nearest 0.5 cm with a flexible steel tape from the junction of the tine and main beam to the tine tip.

Beam Weight.—The beams were removed from the skull within 8 hr of death by sawing at the precise junction of pedicle and burr. Each beam was weighed to the nearest g with a triple-beam balance. The total antler weight is the sum of each beam weight.

Carcass Weights

All collected carcasses with intact antlers were weighed in the laboratory to the nearest 0.1 kg with a double-beam balance. Nearly all weights were obtained within 4 hr of death. Bled weight is the completely intact carcass less the blood loss from gunshot. Eviscerated weight is the intact carcass less all viscera (except the esophagus) and blood loss from gunshot wound.

Browse Yields

On the basis of quantitative studies of foliar cover (Medin and Anderson 1965) and stomach content sample analyses now in progress, we found that true mountain mahogany (*Cercocarpus montanus*), antelope bitterbrush (*Purshia tridentata*), and big sagebrush (*Artemisia tridentata*) were clearly the major winter-range browse species. Their yields were sampled on three approximately 500-acre study areas believed to be representative of the vegetative and topographic characteristics of the lower, middle, and upper portions of the winter range. Estimates were made on established individual plants occurring within a systematic sample of 366 (lower), 299 (middle), and 295 (upper) permanent, 100-ft^2, circular plots. Estimating procedures followed Pechanec and Pickford (1937). Double sampling techniques (Blair 1959) were used in which oven-dry forage weights of individual plants were predicted directly from their estimated green weights.

Deer Numbers

Biannual counts and removal of deer fecal groups were made on the same 100-ft^2 plots used for the browse-yield estimates. Entering the total counts and the assumed average daily defecation rate of 13 groups per deer-day in the formula of Ferguson (1955) provided the estimate of average numbers of deer present on each study area. These were converted to a deer-per-square-mile estimate.

Precipitation

A standard 8-inch diameter precipitation gauge on each of the three winter range study areas was read weekly. All were located on southerly exposures of the same approximate gradient. Anti-freeze and heavy mineral oil prevented freezing and evaporation.

Soil Moisture

Soil samples were collected weekly from the 5–7 inch depth adjacent to the three precipitation gauges and placed in sealed polyethylene bags until analysis. In the laboratory, the soil was sieved through a 2-mm screen, and the percent moisture was measured gravimetrically.

RESULTS

Antler Symmetry

Of 36 paired *t*-tests of left and right antler beam diameters, lengths, and number of points in 16–18 month and 28–30 month old deer, only three showed a significant ($P < 0.05$) difference between the left and right antler beams. Two significant differences are expected at the 5 percent level, and we

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Table 1. Percent frequency of symmetrical, nonsymmetrical, and abnormal antler point categories from 1,674 mule deer sampled at check stations, 1960–65.

Antler Category	Number of Points: Left	Right	Percent of Total by Age-Class (Months): 16–18	28–30	40+
			Number of Deer: 820	372	482
Symmetrical	1	1	11.7	0.0	0.0
	2	2	61.2	13.4	2.1
	3	3	5.9	25.8	12.9
	4	4	0.0	26.3	51.0
	5	5	0.0	1.6	2.3
	6	6	0.0	0.0	0.8
Subtotal			78.8	67.1	69.1
Nonsymmetrical	1	2	5.7	0.0	0.0
	1	3	0.0	0.5	0.0
	1	4	0.0	0.3	0.0
	2	1	4.8	0.5	0.0
	2	3	3.3	8.3	1.0
	2	4	0.0	0.5	0.0
	3	1	0.9	0.0	0.4
	3	2	4.6	5.1	2.3
	3	4	0.2	7.3	4.6
	3	5	0.1	0.3	0.6
	3	6	0.0	0.0	0.2
	4	1	0.0	0.3	0.2
	4	2	0.0	2.2	1.7
	4	3	0.2	5.9	5.4
	4	5	0.0	0.0	4.4
	4	6	0.0	0.0	1.0
	4	7	0.0	0.0	0.2
	5	2	0.0	0.3	0.0
	5	3	0.0	0.3	0.2
	5	4	0.0	0.3	3.9
	5	6	0.0	0.0	0.6
	6	4	0.0	0.0	1.2
	6	5	0.0	0.0	0.6
	6	7	0.0	0.0	0.4
	7	4	0.0	0.0	0.4
	7	5	0.0	0.0	0.2
	7	8	0.0	0.0	0.4
	7	9	0.0	0.0	0.2
	9	10	0.0	0.0	0.2
Subtotal			19.8	32.0	30.5
Abnormal	0	1	0.4	0.0	0.0
	0	2	0.5	0.0	0.0
	0	3	0.1	0.0	0.0
	0	4	0.0	0.0	0.2
	2	0	0.4	0.3	0.0
	3	0	0.0	0.3	0.0
	4	0	0.0	0.3	0.2
Subtotal			1.4	0.9	0.4
Total			100.0	100.0	100.0

Table 2. Percent frequency of antler brow tines by age-class recorded from 1,706 mule deer sampled at check stations, 1960–65.

Age-Class (Months)	One Brow Tine: Left	Right	Two Brow Tines	Brow Tines Absent	Number Deer
16–18	2.0	2.2	1.7	94.1	845
28–30	10.4	10.4	22.5	56.7	374
40+	8.0	8.0	61.0	22.9	487

therefore conclude that the three attributes were essentially symmetrical for these two age-classes. In 25 sets of antlers from deer approximately 15–82 months of age, the paired-*t* test indicated that there was no significant difference ($P > 0.05$) between the weights of left and right antler beams.

Antler Points and Brow Tines

The percent frequencies of 1,674 deer which occurred within 6 symmetrical, 29 non-symmetrical, and 7 abnormal point categories are shown by age-class in Table 1. Of 646 yearlings with symmetrical, normally developed antlers, 14.9 percent had one antler point per beam, and annual percentages of these "spikes" ranged from 6.3 (1964) to 22.6 (1961). Chi-square analysis revealed that these annual proportions differed significantly ($P < 0.01$, 5 df). Deer within the abnormal point categories were those in which the pedicle could not be detected (one yearling) or in which the apparent beam was enlarged and flattened around the pedicle. About 6 percent of 820 yearlings had six antler points and 0.1 percent had eight antler points. There was no annual variation in the number of symmetrical antler point categories. The number of non-symmetrical categories, however, showed considerable annual variation which may be related to sample size. For example, the 433 deer sampled in 1960 were placed in 23 antler-point categories, the 295 deer (1962) in 14, and the 195 (1965)

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Table 3. Inside antler spread (cm) of 1,099 mule deer sampled at check stations, 1960–65.

Age-Class (Months)	Year	N	Mean	SD	95% Conf. Limits Lower	95% Conf. Limits Upper
16–18	1960	184	22.45	4.34	21.82	23.08
	1961	175	21.69	5.04	20.94	22.44
	1962	152	22.76	5.43	21.90	23.62
	1963	113	23.12	4.89	22.22	24.02
	1964	88	24.01	4.48	23.06	24.96
	1965	54	23.72	4.23	22.57	24.87
28–30	1960	84	35.33	7.00	33.82	36.84
	1961	53	34.28	5.33	32.82	35.74
	1962	61	36.08	5.99	34.55	37.61
	1963	25	37.36	5.31	35.17	39.55
	1964	69	39.22	5.58	37.88	40.56
	1965	41	39.07	5.51	37.33	40.81

in 11. Hunter (n.d.:34) reported 10 symmetrical and 17 non-symmetrical antler-point categories from 1,218 Colorado mule deer.

The percent frequency of 1,706 deer with brow tines increased with increasing age (Table 2). Brow tines occurred on 5.9 percent of 845, 16–18-month-old deer and 43.3 percent of 374, 28–30-month-old deer. Annual percentages of 28–30-month-old deer fluctuated from 26.7 (1961) to 55.6 (1965). Chi-square analysis indicated that these annual changes were significant ($P < 0.01$, 5 df). Because the brow tine is an accessory structure developing as a bud and not as a beam bifurcation, its presence or size may indicate relatively robust development. In fact, antler weight (Y) was found to be significantly ($P < 0.01$) correlated ($r = 0.80$) with brow tine length. The regression equation calculated by the method of least squares was $\hat{Y} = -156.07 + 227.26X$ for 25 individual beams from deer 16–121 months in estimated age.

Inside Antler Spread

Antler spread means are described by two age-classes for each year in Table 3. Minimal means occurred in 1961 and their 95 percent confidence limits did not overlap with those of 1964 and 1965. Neither was there overlap between the age-class confidence limits. Nineteen annual means (±SD) for an additional 450 deer of about 40 months and older, segregated into four age classes, ranged from 33.67 ± 6.66 cm (3 deer) to 58.00 ± 7.46 cm (6 deer).

Table 4. Analysis of variance and between-year comparisons of mule deer summed antler beam diameters (cm) sampled at check stations, 1960–65.

Age-Class (Months)	Source of Variation	Degrees of Freedom	Mean Square	F	Annual Comparisons Year	N	Mean[a]	SE
16–18	Total	769			1961	186	3.36	0.05
	Between	5	2.14	8.95*	1965	58	3.60	0.06
	Within	764	0.24		1963	118	3.62	0.05
					1960	173	3.63	0.03
					1962	149	3.64	0.04
					1964	86	3.66	0.04
28–30	Total	362			1961	59	4.69	0.07
	Between	5	3.49	10.32*	1962	63	4.96	0.06
	Within	357	0.34		1960	95	4.97	0.07
					1963	27	5.01	0.10
					1965	45	5.18	0.08
					1964	74	5.38	0.07

* Significant at $P < 0.01$.
[a] The vertical lines encompass mean(s) which are *not* significantly ($P > 0.05$) different.

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Table 5. Analysis of variance and between-year comparisons of mule deer summed antler beam lengths (cm) sampled at check stations, 1960–65.

Age-Class (Months)	Source of Variation	Degrees of Freedom	Mean Square	F	Annual Comparisons			
					Year	N	Mean[a]	SE
16–18	Total	769		9.62*	1961	186	42.64	0.82
	Between	5	840.8		1965	58	46.64	1.04
	Within	764	87.4		1960	173	47.32	0.68
					1963	118	47.58	0.91
					1962	149	48.69	0.65
					1964	86	48.84	0.88
28–30	Total	362		4.37*	1961	59	67.14	1.05
	Between	5	480.9		1963	27	72.67	2.13
	Within	357	110.1		1960	95	72.99	1.39
					1965	45	73.20	1.45
					1962	63	73.35	1.04
					1964	74	75.39	1.12

* Significant at $P < 0.01$.
[a] The vertical lines encompass mean(s) which are *not* significantly ($P > 0.05$) different.

Annual Differences in Antler Development

While measurements of either antler beam could have been used for annual comparisons, the values from each intact set of beams were summed as a possibly less ambiguous measure of antler development. The F-test indicated significant ($P < 0.01$) differences among annual means of beam diameter (Table 4), beam length (Table 5), and number of points (Table 6). Mean comparisons by Duncan's New Multiple Range Test (Steel and Torrie 1960) showed that, in general, means were minimal in 1961 and similar between all other years. These analyses plus the 1961 maximal percentage of yearling spikes and the 1961 minimal percentage of brow tines among 28–30 month old deer cited above, suggest that antler development was relatively poor during 1961.

Table 6. Analysis of variance and between-year comparisons of mule deer summed antler points sampled at check stations, 1960–65.

Age-Class (Months)	Source of Variation	Degrees of Freedom	Square Mean	F	Annual Comparisons			
					Year	N	Mean[a]	SE
16–18	Total	769		5.33*	1961	186	3.60	0.07
	Between	5	4.80		1965	58	3.88	0.14
	Within	764	0.90		1962	149	3.91	0.08
					1960	173	3.93	0.08
					1963	118	3.96	0.08
					1964	86	4.19	0.10
28–30	Total	362		3.25*	1961	59	5.70	0.19
	Between	5	6.50		1965	45	5.93	0.19
	Within	357	2.00		1963	27	6.22	0.31
					1962	63	6.30	0.17
					1960	95	6.41	0.14
					1964	74	6.57	0.17

* Significant at $P < 0.01$.
[a] The vertical lines encompass mean(s) which are *not* significantly ($P > 0.05$) different.

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Table. 7. Annual precipitation, precipitation and average soil moisture prior to the growing season, yields of major browse species, and average deer densities sampled on lower, middle, and upper winter range study areas of about 500 acres each.

Study Area and Elevation (Ft)	Calendar		October Through May			Mean Oven-dry Lb/Acre with 90% Confidence Limits[b]			Average No. Deer per Sq. Mile[c]
	Year	Total Ppt (Inches)	Years	Total Ppt (Inches)	Mean Soil Moisture (% Dry Wt)	*Artemisia tridentata*[a]	*Cercocarpus montanus*	*Purshia tridentata*	
1									
5,800–7,100	1961	20.01	1961–62	7.54	11.6	–	14.8 (11.6–18.0)	29.0 (18.9–39.1)	33
	1962	15.24	1962–63	8.00	8.0	–	10.8 (9.4–12.2)	12.0 (8.9–15.1)	28
	1963	14.69	1963–64	6.65	8.4	–	5.6 (4.2– 7.0)	5.6 (4.2– 6.9)	32
	1964	8.73							
2									
6,600–7,760	1961	21.78	1961–62	7.58	11.3	–	9.9 (7.4–12.4)	43.6 (29.9–57.3)	40
	1962	15.49	1962–63	6.30	6.4	–	3.1 (2.0– 4.2)	8.5 (4.4–12.6)	52
	1963	14.15	1963–64	5.34	6.6	–	5.2 (3.5– 6.9)	13.3 (11.2–15.4)	59
	1964	9.37							
3									
7,440–8,760	1961	28.73	1961–62	12.54	9.6	75.8 (55.2–96.4)	2.9 (0.7– 5.1)	39.3 (24.5–54.1)	39
	1962	18.15	1962–63	7.87	5.9	79.8 (68.5–91.1)	2.0 (0.0– 4.2)	19.3 (14.3–24.3)	28
	1963	19.21	1963–64	7.92	5.4	78.2 (67.8–88.6)	0.5 (0.0– 1.4)	12.4 (10.1–14.7)	61
	1964	14.43							

[a] Does not occur on study area 1 or in measurable amounts on study area 2.
[b] Sampled during September and October, 1962, 1963, and 1964.
[c] Approximately November through April, 1961–62, 1962–63, and 1963–64.

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Table 8. Statistical description and regression equations ($Y = a + bX$) of 4 antler beam variables from collected mule deer, 1961–65. Antler beam measurements are in cm and antler beam weight in g. Antlers were fully developed or in polished bone condition.

Age-Class (Months)	No. Beams	Variable	Mean	SD	C[a]	Variable X	Variable Y	Constants A	Constants B	SE	r
15–18	25	Diameter	1.73	0.26	15.0	Diameter	Length	11.92	6.02	3.30	0.44*
	25	Length	22.32	3.60	16.1	Diameter	No. points	0.85	0.55	0.49	0.27
	25	No. points	1.80	0.54	30.0	Diameter	Wt	–35.50	58.93	20.31	0.62**
	25	Wt	67.28	25.27	37.0	Length	No. points	1.62	0.008	0.50	0.56**
						Length	Wt	54.42	0.58	24.93	0.82**
						No. points	Wt	19.76	26.40	22.01	0.49*
27+	30	Diameter	3.11	0.53	17.0	Diameter	Length	10.07	10.96	3.57	0.86**
	30	Length	44.17	6.83	15.5	Diameter	No. points	0.91	0.81	0.53	0.61**
	30	No. points	3.43	0.71	20.7	Diameter	Wt	–1,201.99	560.45	211.36	0.82**
	30	Wt	541.57	364.73	68.3	Length	No. points	1.13	0.05	0.59	0.50**
						Length	Wt	–1,195.51	39.33	251.13	0.74**
						No. points	Wt	531.61	290.17	312.37	0.52**
15+	55	Diameter	2.48	0.82	33.1	Diameter	Length	–1.05	14.22	4.05	0.94**
	55	Length	34.24	12.30	38.8	Diameter	No. points	31.59	1.07	0.53	0.85**
	55	No. points	2.69	1.02	37.9	Diameter	Wt	–4,730.19	379.62	181.18	0.86**
	55	Wt	325.98	358.51	110.0	Length	No. points	0.26	0.07	0.52	0.86**
						Length	Wt	–496.38	24.02	204.96	0.82**
						No. points	Wt	–378.82	261.91	242.48	0.74**

[a] Coef. variation (%).
* Significant at ($P < 0.05$).
** Significant at ($P < 0.01$).

Environmental and Population Variables

From 1961 through 1964, total annual precipitation, precipitation and mean soil moisture during 8 months prior to the growing season (October–May), and mean browse yields generally decreased (Table 7). Three to fivefold decreases occurred in mean yields of true mountain mahogany and antelope bitterbrush with no detectable change in mean yields of big sagebrush. Indices of average deer population densities indicate concurrently stable or perhaps slightly increasing winter-range populations. The October–May precipitation and soil moisture data were included since Blaisdell (1958:45) reported a significant ($P < 0.05$)

Table 9. Relation of mule deer antler beam weight in grams (Y) to 3 independent variables.

Age-Class (Months)	Variables (X)	No. Beams	r	Regression Equation	SE	Multiple Correlation Coefficients: Calculated	Multiple Correlation Coefficients: Probable[a] Minimum ($P < 0.05$)
15–18	X_2 Beam diameter (cm)	25	0.62	$\hat{Y} = -91.023 + 30.007X_2 + 4.645X_3 + 1.562X_4$	12.56	0.87	0.73
	X_3 Beam length (cm)		0.82				
	X_4 No. points		0.49				
27+	X_2 Beam diameter (cm)	30	0.82	$\hat{Y} = -1278.701 + 479.672X_2 + 6.365X_3 + 13.662X_4$	206.42	0.82	0.66
	X_3 Beam length (cm)		0.74				
	X_4 No. points		0.52				

[a] (Ezekiel and Fox 1959:296).

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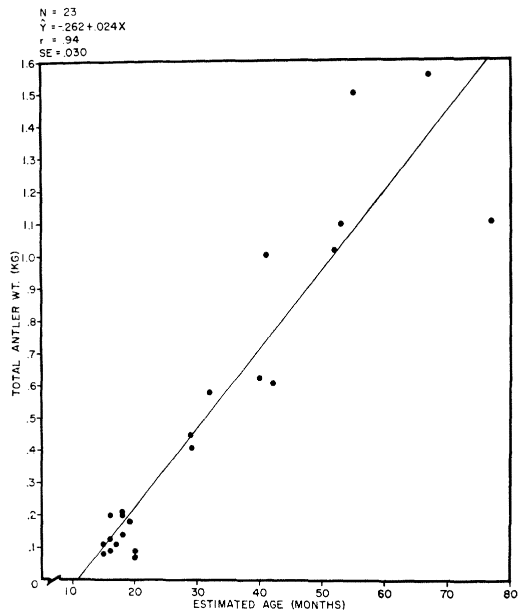

Fig. 1. Relation of total antler weight to estimated age in Cache la Poudre mule deer.

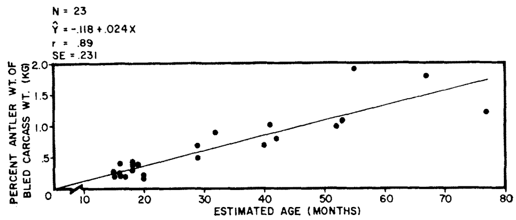

Fig. 2. Relation of total antler weight expressed as a percent of carcass weight to estimated age in Cache la Poudre mule deer.

correlation coefficient (0.668) between precipitation during this period and browse yield within a sagebrush community. Fall soil moisture was significantly ($P < 0.01$) correlated (0.72) with forage yields and significantly ($P < 0.05$) with weight gains (0.52) of cattle the following year in the northern Great Plains (Rogler and Haas 1947:380, 384).

Antler Measurement–Weight Relationships

In Table 8 we present statistical descriptions of antler beam measurements and their weights with regression (B) and simple correlation (r) coefficients of the 4 measurements by 3 broad age-classes. Beam weight is the most variable and beam diameter the least variable. All relationships were found to be linear, most correlation coefficients were highly significant ($P < 0.01$), and among yearlings the best predictor of beam weight was length. The poorest predictor was the number of points. Among deer of about 27 months of age and older, beam diameter was the best predictor, and again the number of points was the poorest predictor of beam weight. Correlation coefficients (r) improved markedly when the entire sample (15+ months) was included, and beam diameter was a slightly better predictor of beam weight than beam length. Among the antler measurements, beam length and diameter were most closely related.

Since none of the simple correlation coefficients of beam measurement–weight relationships were particularly high for reliable prediction, multiple regression equations were computed using beam diameter, length, and number of points (Table 9). These equations did not result in an appreciable improvement in correlation coefficients for yearlings. There was no improvement for deer of 27 months and older. In summary, these analyses show that the measurements employed were only fair predictors of the highly variable antler weight and probably would not reflect any but very large differences in antler development.

Antler Weight–Age–Carcass Weight Relationships

As computed by the method of least squares, total antler weight was strongly and linearly correlated with age (Fig. 1) as was total antler weight expressed as a

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percent of bled carcass weight to age (Fig. 2). Variability increased with increasing age and was particularly pronounced among deer of 40 months and older. A strong and curvilinear correlation was found to characterize the total antler weight–eviscerated carcass weight relationship (Fig. 3). The regression coefficients estimate that, on the average, total antler weight increased about 24 g for each month of age, and the percent of total antler weight of bled carcass weight increased 0.024 percent per month of age. Individual percentages of total antler weight as a percent of bled carcass weight ranged from 0.2 to 1.9. While not included herein because the antlers were still completely in velvet, a fully formed set weighing 4.33 kg from a 73-month-old deer made up 3.9 percent of the bled carcass weight and 5.2 percent of the eviscerated carcass weight. These may approximate the maximum values within the population sampled. Huxley (1931:862) reported that total antler weights expressed as percentages of eviscerated carcass weights ranged from 2.2 to 4.2 in red deer (*Cervus elaphus*), and 1.1 to 1.4 in roe deer. Relative antler weight decreased with increasing carcass weight in the roe deer.

DISCUSSION

Sample Size and Sources of Variability

Tests of sample size adequacy (Snedecor 1946:458–459) for each of the six annual samples, show that samples of all yearling antler attributes were adequate at the chosen level of precision (5 percent of the population mean at $P < 0.05$). In fact, about 58 beam diameters, 129 beam lengths, and 160 antler point counts would have been adequate for any year. However, sample sizes were frequently too small among these same attributes for the 28–30-month-old age-class.

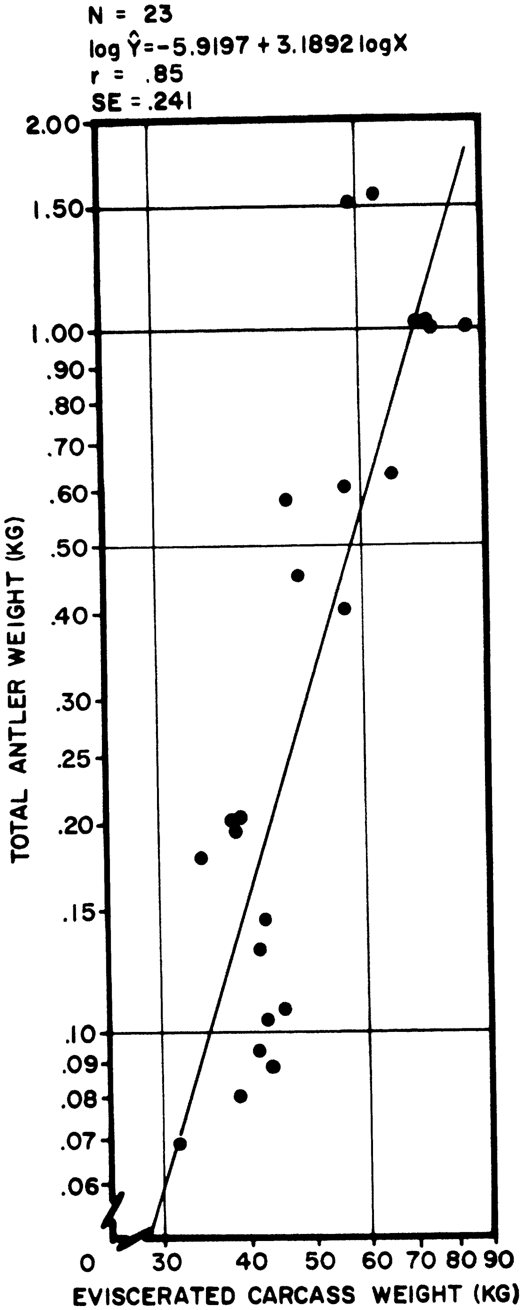

Fig. 3. Relation of total antler weight to eviscerated carcass weight in Cache la Poudre mule deer.

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One possible source of variation among the antler weights herein is the variable moisture content of antler tissue. This moisture content may conceivably be affected by: (1) tissue changes influenced by age and nutritive status interactions and (2) the time elapsed from death to weighing. The first effect has not been demonstrated for any North American cervid, but White (1958) found little variation in either antler moisture content or density among 20 "forked-antler" yearling mule deer from natural range. Antler density of young white-tailed deer remained relatively constant even though the deer were fed a wide variety of experimental diets which resulted in very large differences in antler weights (French et al. 1956:227). The second effect also remains an unknown but since most antlers were weighed within 8 hr of death we assume negligible associated variation.

Antler Development and Environmental Variables

The antler (Tables 4, 5, and 6) and environmental (Table 7) data indicate that minimum antler development occurred during 1961 when maximum precipitation and soil moisture prevailed. However, browse yields were not sampled until the fall of 1962, and the 1961 antler development was presumably a response to the winter forage yields of 1960–61, as postulated by Taber (1958). Lacking environmental or deer population data for 1960, causality for the minimum antler development of 1961 is a matter of conjecture. But if the precipitation–browse yield–antler development response lag theory is applicable, then the maximum precipitation–soil moisture and browse yields of 1961–62, should have resulted in maximum antler development in 1962 with a stable, or perhaps slightly increasing, deer population. Since the antler development of 1962 did not differ significantly from 1963, 1964, or 1965 in any age-class or measurement, it is tentatively concluded that the environmental variables measured were not strongly related to average antler development. This may be due to insufficiently precise measurement not only of antler development, as previously mentioned, but also of the environmental variables. Also likely is the masking effect of other interacting and unmeasured variables, and some possibilities are listed as follows:

1. Even though yields of two winter range browse species declined, the winters were not severe and a variety of other forage of unknown nutritional value was available.

2. Perhaps variations in total diet quality are as important as the quantity of preferred browse. Nutrients such as protein, phosphorus, and calcium are known to be important in antler development (French et al. 1956) and significantly ($P < 0.05$) different calcium levels of selected forage plants did occur on both summer and winter range of the Cache la Poudre deer herd during 1957, 1958, and 1959 (Dietz et al. 1962:31, 48).

3. Since most of the Cache la Poudre population occupies an extensive and apparently excellent summer range during the latter period of antler growth, the following statement by Cowan and Long (1962:59) in reference to white-tailed deer may be pertinent: "The results of these two years' experiments indicate that restricted feeding during the winter months does not result in 'stunting' of antler growth. If feed is plentiful for the months of May, June, and July, antlers will reach normal size."

We believe that even though significant annual differences in antler development may be difficult to detect in migratory mule

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deer at similar altitudes and latitudes, more evidence is needed. Further, antler development may still be a useful comparison of physical condition or reflect environmental differences on a larger scale, for example, comparisons between regions or areas having large differences in habitat or population density.

Antler Weight as a Criterion and Predictor

If mean antler development is used as a criterion of male physical condition or environmental change, we suggest that antler beam weights may be the most reliable and sensitive measure. Five factors recommend the use of single yearling antler beam weights, (1) experimental (French et al. 1956) and empirical (Severinghaus et al. 1950) evidence suggests that yearlings are more responsive to environmental stress than are mature deer; (2) weight of a single antler beam is a direct and relatively precise measure of development; (3) yearlings can be accurately identified; (4) yearlings are available in relatively large sample sizes and their antlers generally have little trophy value; (5) given a coefficient of variation similar to the Cache la Poudre sample (37 percent), about 210 antler beam weights would be sufficient to be within 5 percent of the population mean at $P < 0.05$.

The applicability of the Cache la Poudre antler weight–carcass weight–age relationships to other migratory mule deer populations requires further study. It may be that different populations will require development of specific prediction equations.

Some possible management applications of the resulting prediction equation would be to: (1) estimate eviscerated carcass weight of antlered males with intact antlers when other body parts are missing; (2) estimate post-season age structure of antlered males on densely populated winter range by weighing a sample of shed antler beams. Such data may aid in assessing the effects of habitat manipulation, harvest density, or climatic factors on male age structure.

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Received for publication December 3, 1968.

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